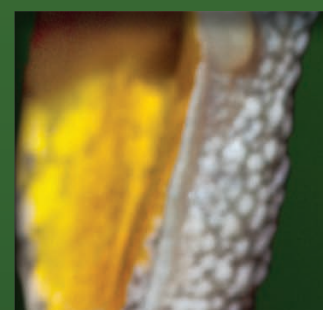


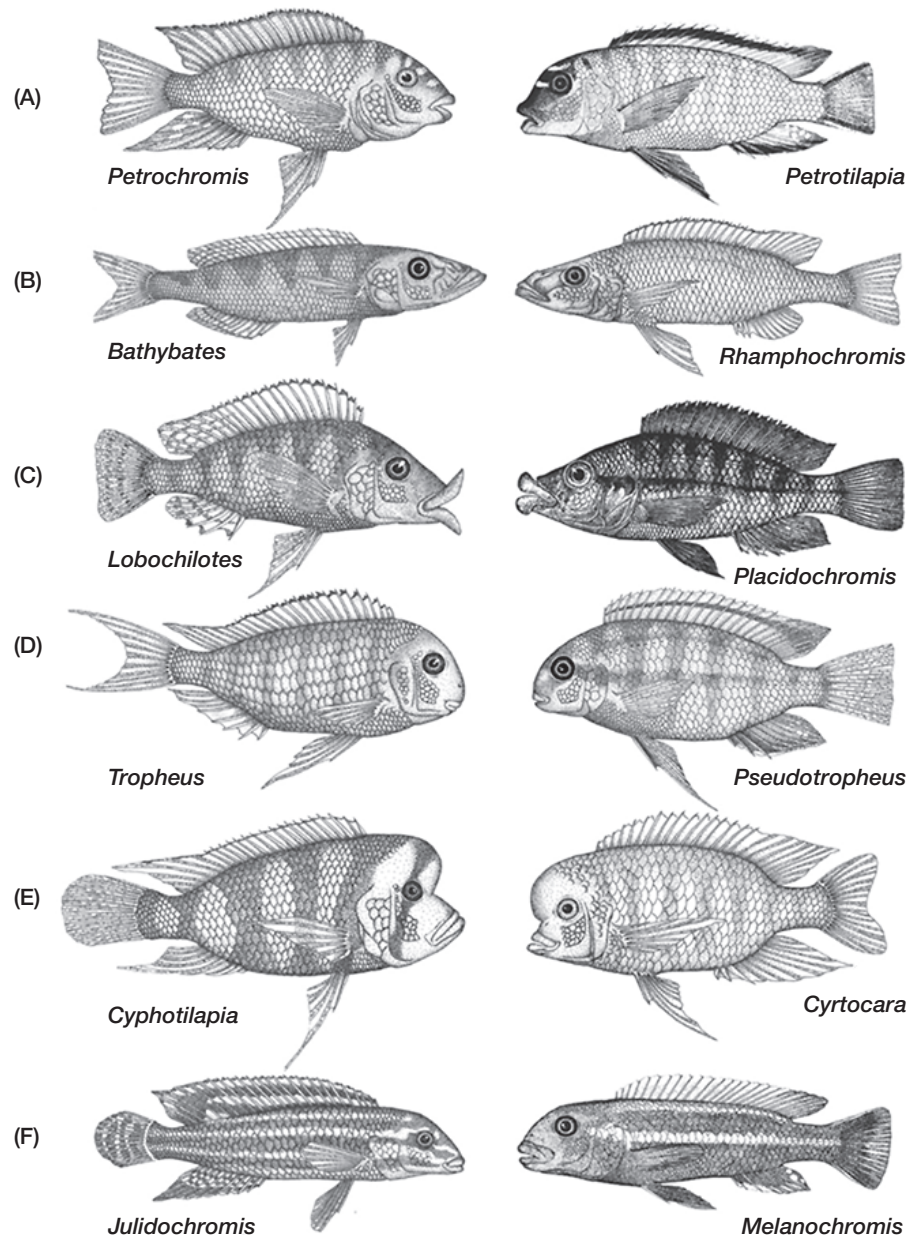
Species and Speciation

In the Rift Valley of eastern Africa, just south of the equator, lie three great lakes and many smaller ones. Lakes Tanganyika and Malawi are deep and old, having been formed by the separation (rifting) of two continental plates. Lake Victoria, in contrast, is broad and shallow, lying in a basin that was dry only 15,000 years ago. These lakes harbor a few species of catfishes, spiny eels, and other fish families, but more than 90 percent of all the fish species are cichlids, a family that includes species well known to tropical fish hobbyists. Lake Tanganyika has at least 250 species of cichlids, Lake Victoria between 450 and 530 species, and Lake Malawi at least 480 species [89]. (The American Great Lakes, in comparison, have only about 175 species of fishes, of all kinds.) These cichlid fishes are extraordinarily diverse in coloration, form, feeding habits, and habitat use (**FIGURE 9.1**). Different species eat insects, snails, detritus, rock-encrusting algae, aquatic plants, phytoplankton, zooplankton, baby fishes, and larger fishes. Some species are specialized to feed on the scales of other fishes, and one has the gruesome habit of plucking out other fishes' eyes. The teeth of some closely related species differ more than do those of some whole families of fishes. Many of these habits and morphologies have evolved convergently in the different lakes [45]. Phylogenetic analyses show that the 250 cichlids in Lake Tanganyika have evolved from at most 16 original species. The cichlids of Lake Victoria have multiplied faster than any other group of vertebrates on Earth: the 450-plus species evolved from just 5 original ancestral species in perhaps only 15,000 years [95, 105].



◀ A male gray tree frog inflates his vocal sac as he calls to attract females. Female frogs respond almost exclusively to their own species' calls, which are a barrier to interbreeding. Male calls differ between two morphologically indistinguishable species of gray tree frogs in eastern North America. *Hyla chrysoscelis* has 12 pairs of chromosomes, whereas *H. versicolor* is a tetraploid, with 24 pairs.

FIGURE 9.1 Examples of the diversity of cichlid fishes in Lakes Tanganyika (at left) and Malawi (at right). Ecologically and morphologically similar forms have evolved independently in both lakes. (A) Rock-dwelling species with rasping jaws. (B) Open-water fish-eaters. (C) Fleshy-lipped species that suck prey from crevices. (D) Rock-dwellers. (E) Hump-headed species. (F) Slender, striped species. (From [2]).



What caused this explosion of diversity? Do the number and ecological variety of species depend only on current ecological conditions, such as how many different kinds of resources can sustain different species? Or do they reflect the rate at which new species have arisen? Why should the rate of speciation have been so high in this fish family, and only in these lakes? Has speciation been caused by the fishes' mating patterns? By sexual selection on coloration? By adaptation to different ecological niches? By genetic drift? Fundamentally, what we want to know is: How do new species form?

Darwin first came to believe in evolution when he realized that different islands in the Galápagos archipelago harbor different forms of mockingbirds and a variety of similar finches. That these forms were similar, yet subtly different, could most plausibly be explained by supposing that they had descended, with slight modifications, from a common ancestor. Pursuing this reasoning, Darwin concluded that all species of birds—indeed all species of animals, and finally all living things—may have originated by successive branching of lineages throughout the history of life, from a single common ancestor. Modern research has affirmed that this is indeed how the enormous diversity of organisms arose. The forks in the great Tree of Life were caused by **speciation**, the process by which one species gives rise to two.

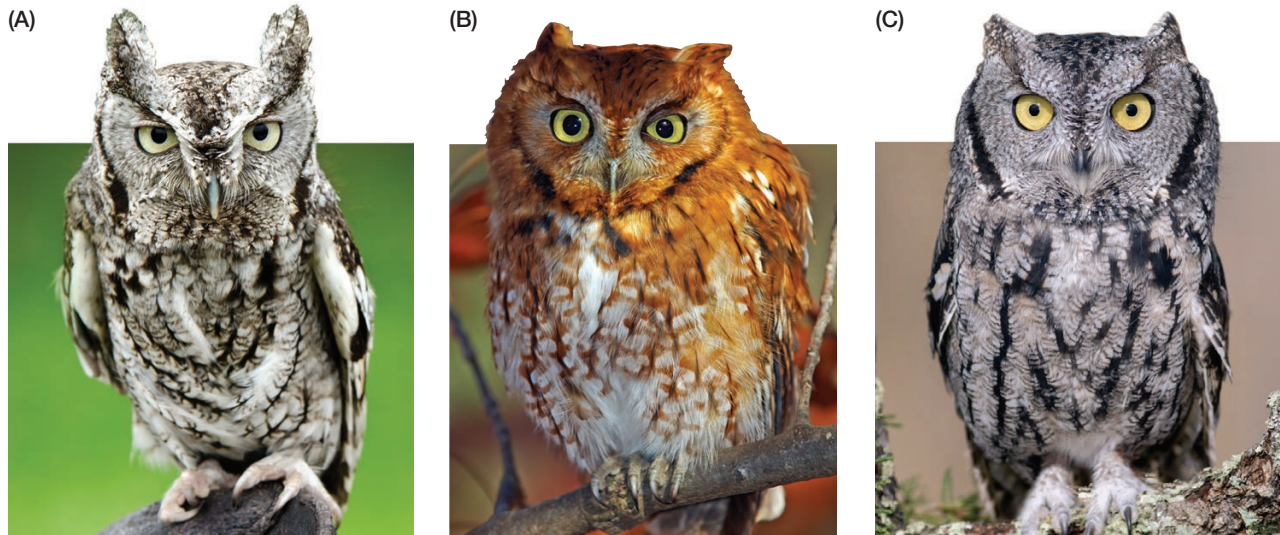


FIGURE 9.2 Can you distinguish the species? (A, B) Gray and rufous morphs of the eastern screech owl (*Megascops asio*). (C) The western screech owl (*Megascops kennicottii*).

What Are Species?

Several definitions of “species”—which is Latin for “kind”—are used by biologists. It is important to bear in mind that a definition is not true or false, because the definition of a word is a convention. Probably no single definition of “species” suffices for all the contexts in which a species-like concept is used.

For Linnaeus and other early taxonomists, species were simply groups of organisms that could be distinguished. But as knowledge of organisms grew, this criterion became inadequate. For example, two kinds of small owls in eastern North America look very different: one is gray and the other bright reddish brown (**FIGURE 9.2A,B**). Nevertheless, they are clearly the same species: the two forms sound the same, they interbreed, and a brood may include both color forms—which are a simple one-locus polymorphism (with rufous dominant over gray). But the gray form of this species, the eastern screech owl (*Megascops asio*), is almost indistinguishable in appearance from another owl that has a very different voice and that is recognized as a distinct species—the western screech owl (*M. kennicottii*; **FIGURE 9.2C**). The two species can be completely distinguished by mitochondrial DNA [77], indicating that even though they coexist in Texas, there is little or no gene flow between them. They are separate *gene pools*.

Cases such as the screech owls led to the concept of species as groups of individuals that interbreed. Ernst Mayr [55] formalized this idea in what he called the **biological species concept (BSC)**, defined as follows: “*Species are groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups.*” **Reproductive isolation** means that any of several biological differences between the groups greatly reduce gene exchange between them, even if they are not geographically separated. The BSC does not require that species be 100 percent reproductively isolated—there can be a little genetic “leakage” between species through hybridization. Although genetic and phenotypic differences do not *define* species according to the BSC, those differences enable us to *recognize* and distinguish them. Note that an inability to form hybrid offspring, or sterility of hybrids, is *not* a necessary criterion of species: it is only one of many ways in which gene exchange may be reduced or prevented.

The biological species concept was developed partly to acknowledge variation, both within a single population (such as the color morphs of the eastern screech owl) and among different geographic populations, which often show evidence of

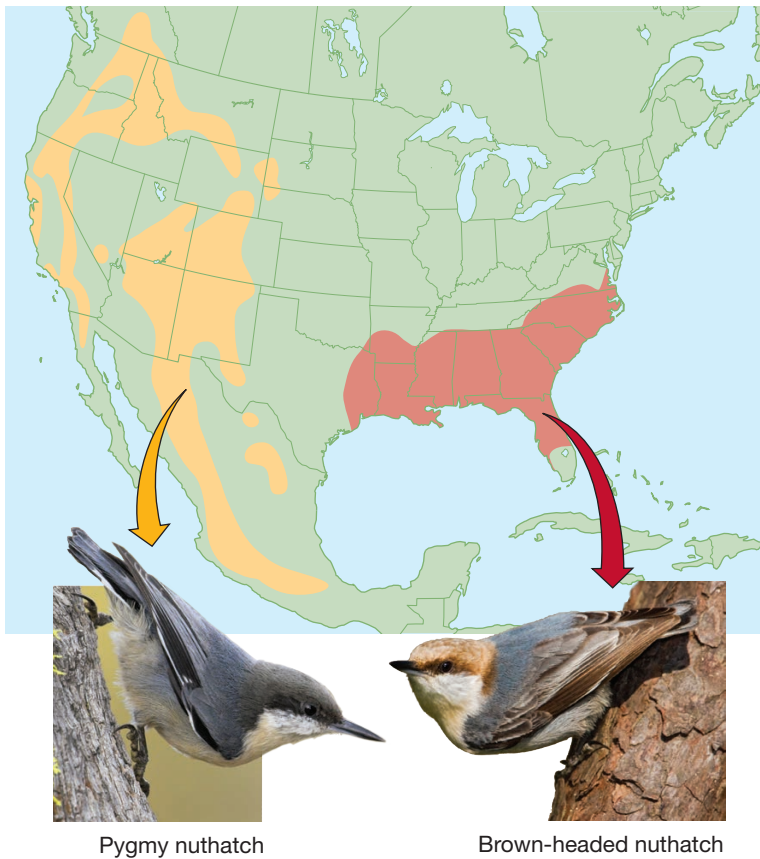


FIGURE 9.3 The geographic ranges of the pygmy nuthatch (*Sitta pygmaea*, left), in western North America, and of the brown-headed nuthatch (*Sitta pusilla*, right), in the southeastern United States, are separated by hundreds of miles in which neither bird occurs. They differ in voice and subtly in color pattern. It is difficult to tell if they are different biological species.

interbreeding where they meet. The BSC also recognizes cases of “sibling species” (such as the gray forms of the two screech owls), which are almost identical in appearance and are often discovered by differences in ecology, behavior, chromosomes, or genetic markers. The discovery that the European mosquito *Anopheles maculipennis* is actually a cluster of nine sibling species had great practical importance because some transmit human malaria and others do not [3, 39]. The term “sibling species” differs from **sister species**, which are two species descended from a single ancestral species, and are therefore one another’s closest relatives.

The biological species concept is the most widely used definition among biologists, and it can be applied to the majority of sexually reproducing species alive on Earth. It does, though, have limitations. Reproductive isolation evolves gradually, as we will see. So interbreeding versus reproductive isolation is not an either/or, all-or-none distinction. Nevertheless, there are countless examples of closely related forms that occur in the same area, can be distinguished by genetic and phenotypic differences, and interbreed very little or not at all. They are unequivocally distinct, real species.

The greatest practical limitation of the BSC is in determining whether populations that are geographically separated (**allopatric**) belong to the same species (**FIGURE 9.3**). The BSC requires that we make a judgment call as to whether they would interbreed if they came into contact under natural conditions. Climate change in the past and human changes to the environment at present have brought formerly isolated populations together. In some such cases, the popula-

tions remained distinct, but in other cases they interbred, showing that they were not fully distinct species. One could test for reproductive isolation experimentally, for example in the lab or garden, but this is impractical or even impossible to do with many species (e.g., giant squids). Moreover, some species that mate under artificial conditions will not do so in nature, and hybrid offspring that are viable and fertile in the lab may not survive in nature. In practice, deciding whether geographically isolated populations are species is at times somewhat arbitrary. Commonly, allopatric populations have been classified as species if their differences in phenotype or in DNA sequence are as great as those usually displayed by species in the same group that are **sympatric** (in the same location) [103]. A similar approach is taken with classifying fossils into species, since paleontologists cannot study the mating behavior or hybrid survival of extinct ammonites or dinosaurs.

Another limitation of the BSC is that it does not apply to organisms that do not reproduce sexually. Bacteria pose particular challenges. Although they do not have meiotic sex, they do exchange genetic material in other ways. Species of bacteria, such as *Escherichia coli* and *Salmonella typhimurium*, were traditionally recognized by differences in their metabolic capabilities. More recently, genetic similarity has been used to group individuals into species. Although bacteria can acquire new genes from even distantly related organisms, most homologous recombination (“sex”) occurs within traditionally recognized species [66].

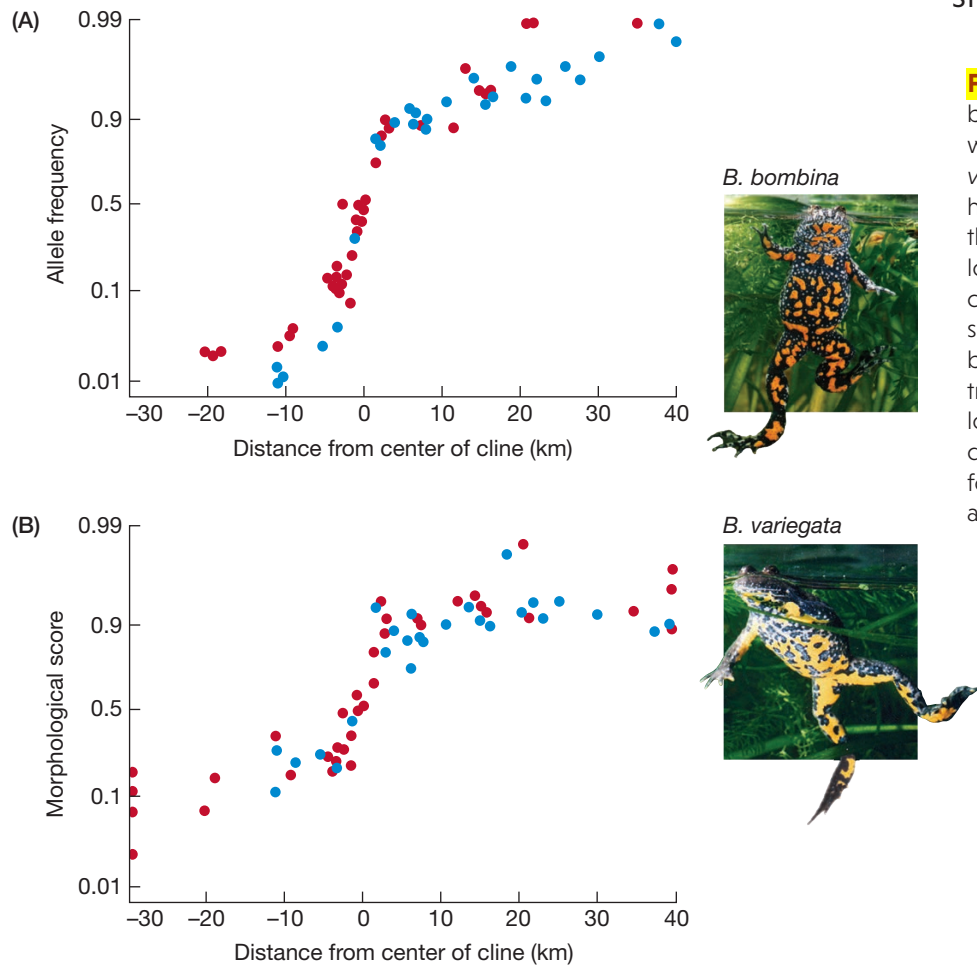


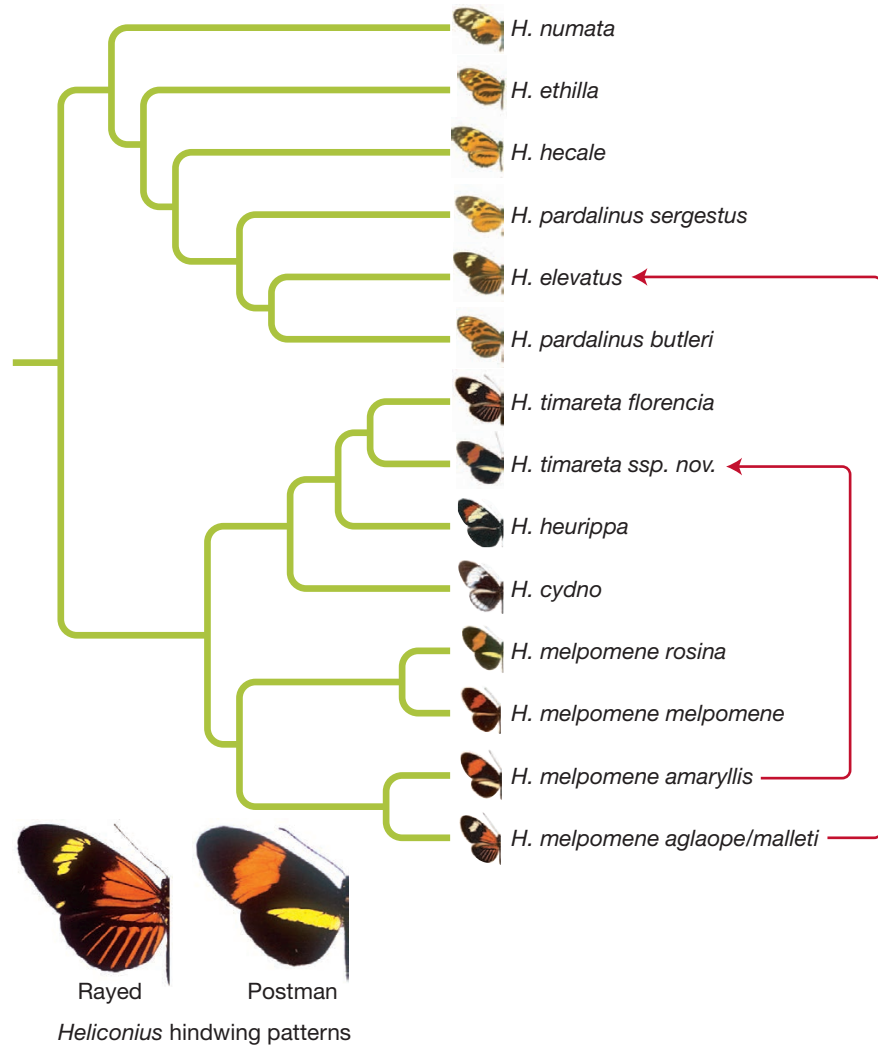
FIGURE 9.4 The eastern European fire-bellied toad (*Bombina bombina*) and the western European yellow-bellied toad (*B. variegata*) meet and interbreed in a narrow hybrid zone. The two species differ in loci that code for enzymes and several morphological features. (A) Average allele frequency at six enzyme loci. (B) A morphological score based on seven characters. Red and blue dots represent two different 60-km transects in Poland. The clines in enzyme loci and morphological features are coincident, suggesting that this hybrid zone was formed by contact between two formerly allopatric populations. (After [100].)

These and other considerations have inspired several alternative species definitions. Some systematists prefer the **phylogenetic species concept (PSC)**, which emphasizes species as the outcome of evolution—the products of a history of evolutionary divergence. In one widely accepted definition, lineages are different species if they can be distinguished: a phylogenetic species is *an irreducible (basal) cluster of organisms diagnosably different from other such clusters, and within which there is a parental pattern of ancestry and descent* [17].

The phylogenetic and biological species concepts have different uses, and tend to be used by different groups of researchers. The PSC can be useful for classification, because unlike the BSC, it can be applied to allopatric populations, such as those on different islands, in which reproductive isolation is difficult or impossible to assess. Although some systematists use the PSC in classifying organisms, most evolutionary biologists use one or another variant of the BSC, because they view the evolution of reproductive isolation as the key event that enables sexually reproducing lineages to evolve independently and generate biological diversity. Without the evolution of reproductive isolation, there would be only one (or at most a few spatially separated) species of cichlid in each of those African lakes.

No matter which species concept is adopted, some populations of organisms cannot be unambiguously assigned to one species or another, because the features that distinguish species (by any definition) evolve gradually. There exist graded levels of gene exchange among adjacent (**parapatric**) populations and sometimes between more or less distinct populations that are sympatric. Species as recognized by the BSC are ambiguous in **hybrid zones**, which exist where genetically distinct populations meet and interbreed to a limited extent, but in which there exist partial barriers to gene exchange (**FIGURE 9.4**). Hybridization occurs, at least

FIGURE 9.5 Advantageous alleles have spread by introgression between distantly related species of *Heliconius* butterflies in South America. The phylogeny is based on many genes. The DNA sequence of two genes that control color pattern shows that *H. timareta* ssp. nov. acquired the “postman” pattern in the hindwing from *H. melpomene amaryllis*, and that *H. elevatus* acquired the “rayed” hindwing pattern from *H. melpomene aglaope/malleti*. (From [35]; large wing images courtesy of J. Mallet.)



occasionally, among sympatric species in many groups of plants and animals [51], and genes are sometimes incorporated into the gene pool of one species from another, a process called **introgression** (or introgressive hybridization). Some such genes may enhance adaptation [1]. For instance, *Heliconius* butterflies are distasteful to predators and have warning coloration: predators do not attack butterflies with this pattern after one or two experiences in which they learn to associate the coloration with distastefulness. Alleles that determine part of the color pattern of the wings of certain *Heliconius* species have spread among even distantly related species (**FIGURE 9.5**).

Biological species are seldom distinguished in practice by directly testing their propensity to interbreed or their ability to produce fertile offspring. Indeed, this is usually not necessary. Morphological and other phenotypic characters are the usual evidence used for diagnosing sympatric species (**FIGURE 9.6**), because they can serve as *markers* that indicate reduced gene flow—that is, reproductive isolation—among sympatric populations. If a sample of sympatric organisms falls into two discrete clusters that differ in multiple characters, it is likely to represent two species. In modern studies, genetic markers are often used to reveal the existence of two or more sympatric species. A polymorphic locus that shows few heterozygotes, and so departs strongly from Hardy-Weinberg equilibrium, is a signal that there are likely to be more than one species. (**BOX 9A** provides an example.)

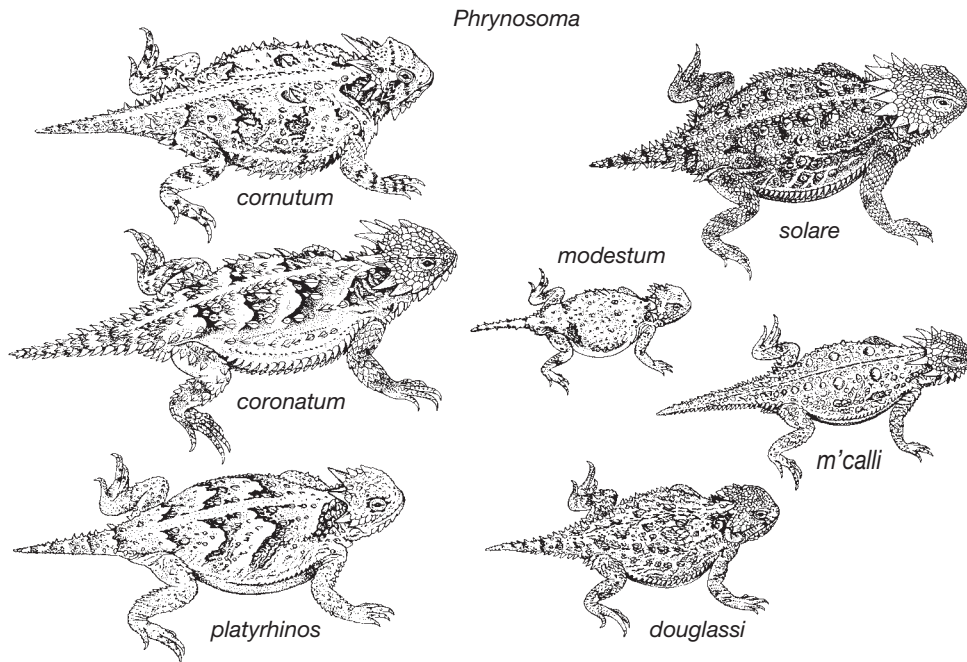


FIGURE 9.6 An example of species distinguished by morphological characters. These seven species of horned lizards (*Phrynosoma*) from western North America can be distinguished by differences in the number, size, and arrangement of horns and scales as well as body size and proportions, color pattern, and habitat. Good scientific drawings can often show detailed features better than photographs can, especially when the critical features are subtle. (From [98].)

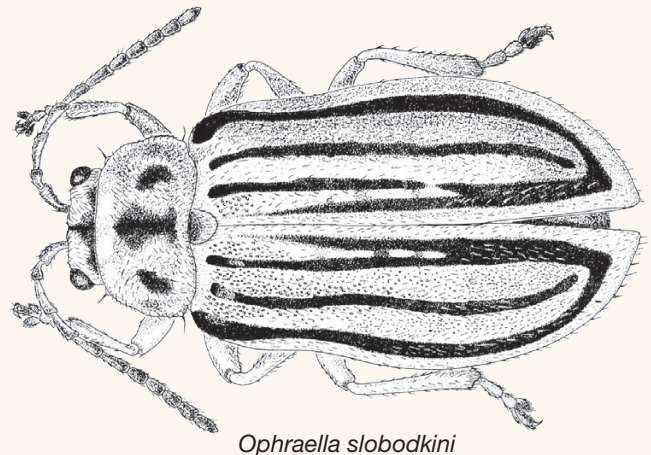
BOX 9A

Diagnosis of a New Species

Each species in the leaf beetle genus *Ophraella* feeds on one species or a few related species of plants. *O. notulata*, for example, has been found feeding only on two species of *Iva* along the East Coast of the United States. This species is most readily distinguished from other species of *Ophraella* by the number and pattern of dark stripes on each wing cover.

Some leaf beetles found in Florida closely resembled *O. notulata* but were collected on ragweed, *Ambrosia artemisiifolia*. This host association suggested the possibility that these beetles were a different species. In a broader study of the genus, one of the authors of this book (DJF) collected samples of beetles from both *Ambrosia* and *Iva* throughout Florida and examined them by enzyme electrophoresis [30]. He found consistent differences in allele frequencies between samples from *Iva* and from *Ambrosia* at three loci, even in samples from both plants in the same locality. In the most extreme case, one allele had an overall frequency of 0.968 in *Ambrosia*-derived specimens, but was absent in *Iva*-derived specimens, in which a different allele had a frequency of 0.989. No specimens had heterozygous allele profiles that would suggest hybridization. Later study showed differences in mitochondrial DNA as well. Thus these genetic markers were evidence of two reproductively isolated gene pools.

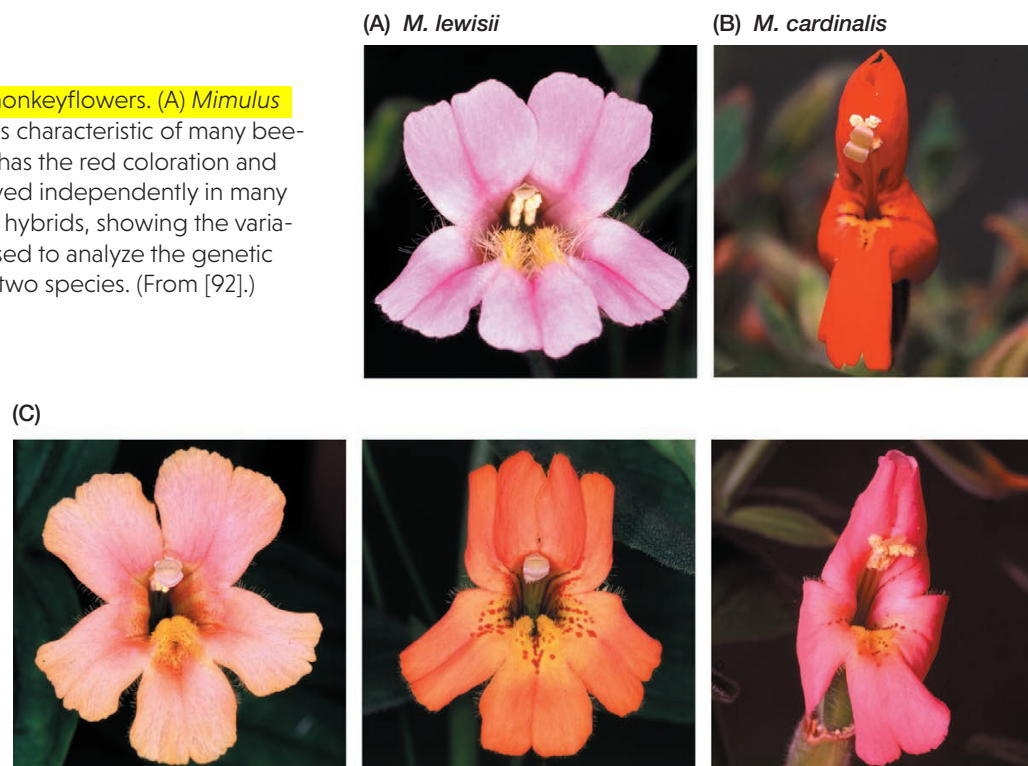
A careful examination then revealed average differences between *Ambrosia*- and *Iva*-associated beetles in a few



Ophraella slobodkini

morphological characters, such as the shape of one of the mouthparts and the relative length of the legs. Later studies showed that adults and newly hatched larvae strongly prefer their natural host plant (*Ambrosia* or *Iva*) when given a choice, and that the beetles mate preferentially with their own species. In laboratory crosses, viable eggs were obtained by mating female *Ambrosia* beetles with males from *Iva*, but not the reverse. Few of the hybrid larvae survived to adulthood, and none laid viable eggs. Based on all of this evidence, the author concluded that the *Ambrosia*-associated form is a distinct species, and he named it *Ophraella slobodkini* in honor of the ecologist Lawrence Slobodkin.

FIGURE 9.7 Pollinator isolation in monkeyflowers. (A) *Mimulus lewisii* has the broadly splayed petals characteristic of many bee-pollinated flowers. (B) *M. cardinalis* has the red coloration and narrow, tubular form that have evolved independently in many bird-pollinated flowers. (C) Some F_2 hybrids, showing the variation that Schemske and Bradshaw used to analyze the genetic basis of differences between these two species. (From [92].)



Reproductive Isolation

Gene flow between biological species is prevented by biological differences called **reproductive isolating barriers (RIBs)**, also referred to as **isolating mechanisms**. Under the biological species concept, speciation is the evolution of biological barriers to gene flow, and so understanding the evolution of reproductive isolating barriers tells us how new species evolve.

The total degree of reproductive isolation between two species may result from several RIBs that act in sequence—and some potential RIBs may not come into play. For example, the monkeyflower *Mimulus lewisii* is distributed in the Sierra Nevada of California at higher elevations than its close relative *Mimulus cardinalis*, although they both occur at intermediate elevations [92]. *Mimulus lewisii* has pink flowers with a wide corolla and is pollinated by bees, whereas *M. cardinalis* has a narrow, red, tubular corolla and is pollinated by hummingbirds (**FIGURE 9.7**). Although almost no hybrids are found where the species occur together, the species can be readily crossed, and they produce viable, fertile hybrids.

To understand the roles played by different isolating barriers between these species, Douglas Schemske, Toby Bradshaw, and their colleagues performed a massive field experiment. They bred a large number of F_2 hybrids and planted them in an area where the two species coexist. The F_2 s have far greater phenotypic variation than the parental species, and they have novel combinations of traits. By amplifying the variation this way, the researchers were able to determine which of 12 floral traits that distinguish the parental species are important to reproductive isolation. They went further by using a quantitative trait loci (QTL) study (see Chapter 6) to reveal the genes underlying those traits [8]. At least four traits affect the type of pollinator that is attracted to a flower, which in turn determines which individuals exchange genes. The difference between the species in some of these traits is based on as few as one to as many as six QTL, so a change to one or a few genes can greatly affect reproductive isolation.

The investigators were able to quantify the contribution that different mechanisms make to reproductive isolation, in sequence (**FIGURE 9.8**). Separation by elevation alone reduces gene exchange by 59 percent. Among plants living at the same

elevation, pollinator fidelity alone is 98 percent effective. If a flower receives both species' pollen, the conspecific pollen (that is, pollen from the same species) fertilizes the ovules at least 70 percent of the time. The germination of F_1 hybrid seeds is reduced by 20 percent compared with nonhybrids, but a hybrid seed that does germinate is just as viable. Hybrids produce fewer seeds, however, and they produce much less viable pollen. But because isolation by elevation and pollinator behavior is so great, the later barriers—reduced production, viability, and fertility of hybrids—hardly come into play at all.

The *Mimulus* species illustrate some of the many kinds of RIBs (TABLE 9.1). **Prezygotic barriers** reduce the likelihood that hybrids are formed. These include such factors as separation of the species in different habitats, pollination by different animals, mating at different seasons, mating preferentially with conspecifics, and failure of gametes to unite even if mating occurs. **Postzygotic barriers** reduce gene exchange between populations even if hybrid zygotes are produced. They consist of reduced hybrid viability (survival) or reproduction (fertility). Both classes of barriers are often asymmetric: for example, females of species A may be less inclined to mate with males of species B than females of B are to mate with males of A [40], or F_1 hybrids between the species may differ in viability, depending on the direction of the cross [104, 108].

Since prezygotic isolating mechanisms act before postzygotic mechanisms, they have a greater opportunity to restrict gene flow. A second reason why the distinction between prezygotic and postzygotic mechanisms is useful is that different kinds of selection act on them, as we will see shortly.

It is often difficult to tell which isolating barrier was the original cause of speciation. A character difference that contributes to reproductive isolation now may have evolved partly in geographically segregated populations before they became

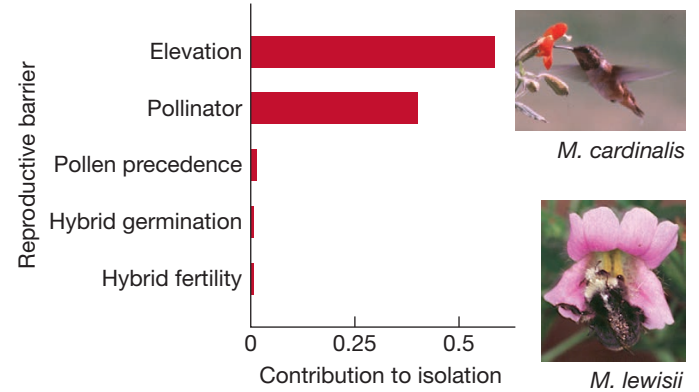


FIGURE 9.8 Relative contributions of successively acting isolating mechanisms between the monkeyflowers *Mimulus lewisii* and *M. cardinalis*. Elevational separation and pollinator isolation account for almost all the reproductive isolation. In places where both species occur, pollinators provided almost complete reproductive isolation. (After [80]; photos courtesy of D. W. Schemske and H. D. Bradshaw, Jr.)

TABLE 9.1 A classification of isolating barriers

- I. Premating barriers: features that impede transfer of gametes to members of other species
 - A. Ecological isolation: potential mates do not meet
 1. Temporal isolation: species breed at different seasons or times of day
 2. Habitat isolation: species mate and breed in different habitats
 3. Immigrants between divergent populations do not survive long enough to interbreed
 - B. Potential mates meet but do not mate
 1. Sexual isolation in animals: individuals prefer mating with members of their own species
 2. Pollinator isolation in plants: pollinators do not transfer pollen between species
- II. Postmating prezygotic barriers: mating occurs, but zygotes are not formed
 - A. Mechanical isolation: reproductive structures of the sexes do not fit
 - B. Copulatory isolation: female is not stimulated by males of the other species
 - C. Gametic isolation: failure of fertilization
- III. Postzygotic barriers: hybrids are formed but have reduced fitness
 - A. Extrinsic: hybrids have low fitness for environmental reasons
 1. Ecological inviability: hybrids are poorly adapted to both of the parental habitats
 2. Behavioral sterility: hybrids are less successful in obtaining mates
 - B. Intrinsic: low hybrid fitness is independent of environmental context
 1. Hybrid inviability: reduced survival is due to genetic incompatibility
 2. Hybrid sterility: reduced production of viable gametes

Source: After [15], in part.

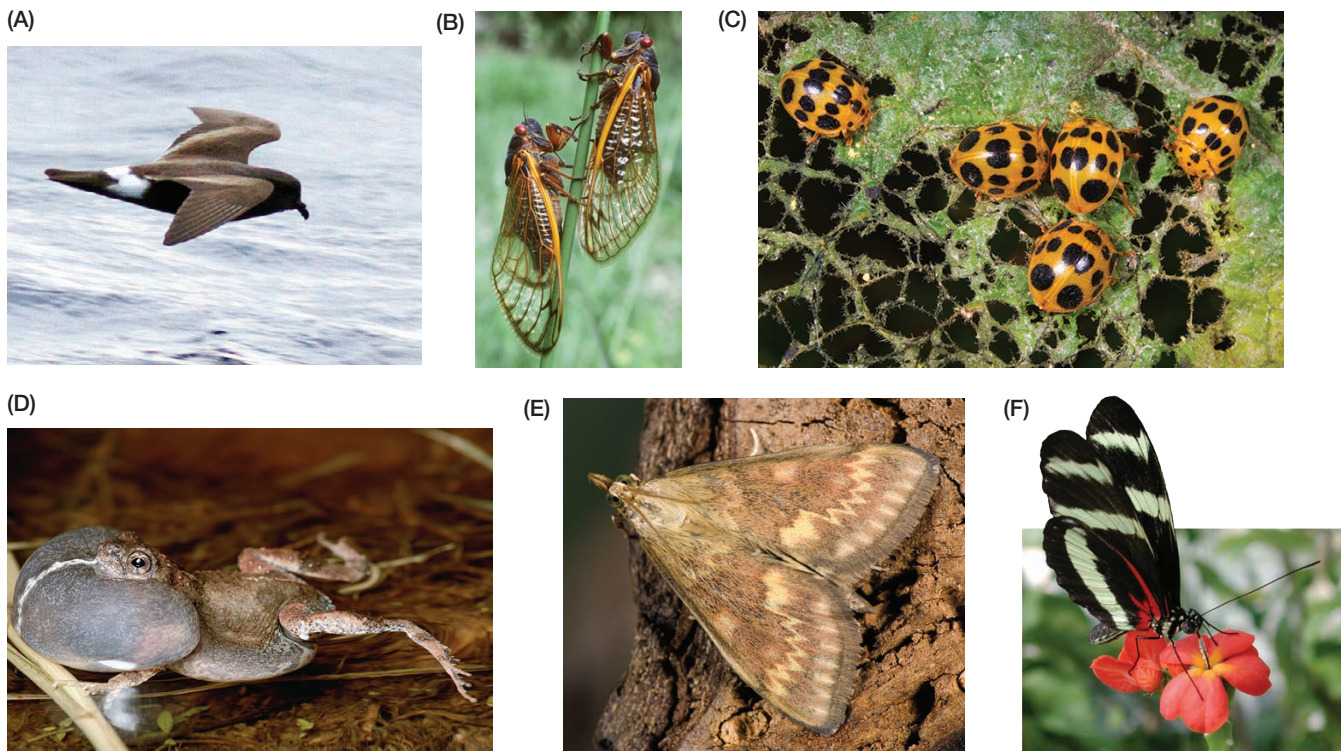


FIGURE 9.9 Prezygotic isolation takes many forms, illustrated by some species that have been extensively studied. (A–C) Three modes of prezygotic isolation. (A) Seasonal isolation: the band-rumped storm-petrel (*Oceanodroma castro*) includes two genetically different populations that mate at different times of year [28]. (B) Temporal isolation: related species of periodical cicadas (*Magicicada*) have either 17- or 13-year life cycles, and rarely emerge in the same year [10]. (C) Ecological isolation: closely related species of ladybird beetles (*Henosepilachna*) feed and mate

on different species of plants [41]. (D–F) Examples of sexual isolation based on different sensory modalities. (D) Female *Physalaemus* frogs respond almost exclusively to the calls of conspecific males [88]. A calling male *P. pustulosus* is shown here. (E) In moths and many other animals, sexual isolation is based on different chemical signals. Two forms of the European corn borer (*Ostrinia nubilalis*) are strongly isolated by responses of males to different female sex pheromones [85]. (F) Males of *Heliconius pachinus* recognize conspecific females by their wing color pattern [48].

different species, partly during the process of speciation, and partly after the reproductive barriers evolved. Because genetic differences continue to accumulate long after two species achieve complete reproductive isolation, some of the genes, and even some of the traits, that now confer reproductive isolation may not have been instrumental in forming the species in the first place. Such information can be obtained by studying populations that have achieved reproductive isolation only very recently.

Prezygotic barriers

In many plants and animals, prezygotic barriers are the most important isolating mechanisms. There are many kinds of barriers, depending on the biology of the organism (**FIGURE 9.9**). Species may be temporally isolated by mating at different times of year, or even in different years. **Ecological isolation** results when ecological differences, for example habitat preference, contribute to genetic barriers [64, 93]. For example, two Japanese species of herbivorous ladybird beetles (*Henosepilachna*) feed on different genera of host plants (*Cirsium* and *Caulophyllum*). Each species mates exclusively on its own host plant, and this ecological segregation appears to be the only barrier to gene exchange [41]. **Sexual isolation** is an important barrier to gene flow among sympatric species of animals that frequently encounter each other but simply do not mate. Commonly, females will not respond to inappropriate male vocalizations or other display signals. Many birds, fishes, and jumping spiders are sexually isolated by visual signals. In many groups of animals, sexual isolation is based on differences in sex pheromones.

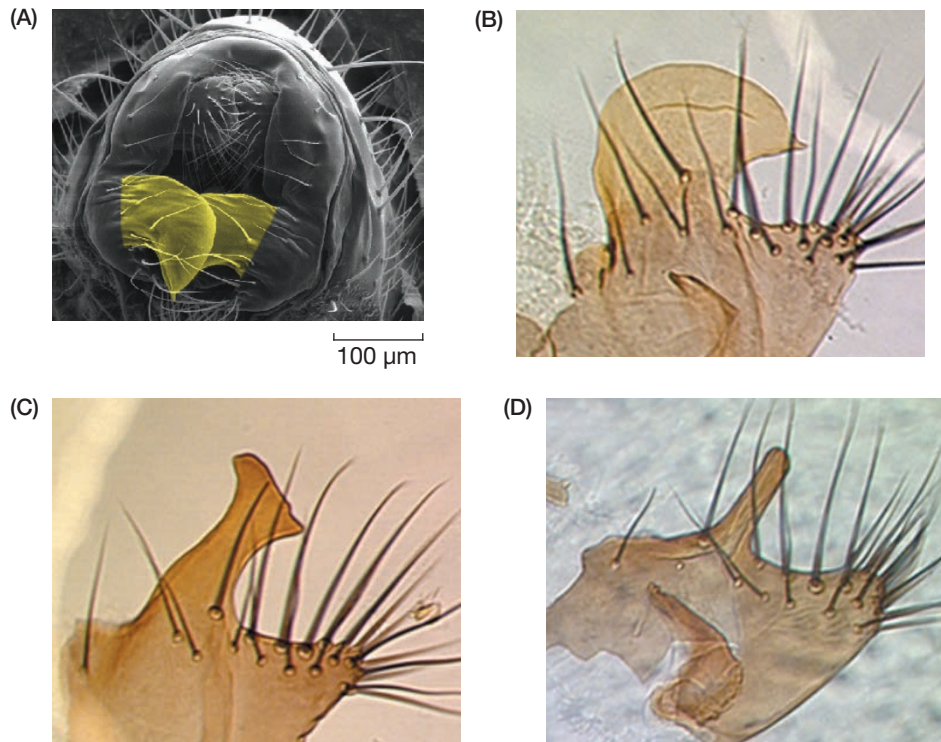


FIGURE 9.10 Differences in genitalia can contribute to reproductive isolation between species if copulation between them occurs. (A) The genital arch in male *Drosophila* is involved in transferring sperm to females. Its shape differs among closely related species, as the close-ups show: (B) *D. sechellia*, (C) *D. mauritiana*, (D) *D. simulans*. This morphological feature is almost the only one by which these species differ. (A from [53]; B, C, and D courtesy of J. R. True.)

Gametic isolation occurs when gametes of different species fail to unite. This barrier is important in many externally fertilizing species of marine invertebrates that release eggs and sperm into the water. Because cell surface proteins determine whether or not sperm can adhere to and penetrate an egg, divergence in these proteins can result in gametic isolation [69]. Among species of abalones (large gastropods), the failure of heterospecific eggs and sperm to unite is related to the high rate of divergence in the amino acid sequences of both lysin (the sperm protein that dissolves the egg's vitelline envelope) and the vitelline envelope protein with which it interacts (see Chapter 10) [32]. In cases that fall in between premating and postmating isolation, mating occurs but fertilization does not. In many groups of insects and some other taxa, the genitalia of related species differ in morphology. There is evidence that females terminate mating, and prevent transfer of sperm, if a male's genitalia do not provide suitable tactile stimulation (FIGURE 9.10) [22].

Postzygotic barriers

Postzygotic barriers consist of reduced survival or reproductive rates of hybrid zygotes that would otherwise backcross to the parent populations. These barriers can be classified as either extrinsic or intrinsic, depending on whether or not their effect depends on the environment. Intrinsic isolation is based on interactions between genes from two populations, and is often more permanent than extrinsic isolation.

Extrinsic postzygotic isolation is often based on reduced survival because of ecological factors. In some cases, the parent species are adapted to different environments; the hybrid may be poorly adapted to both. A simple example is provided by hybrids between species of *Heliconius* butterflies that are distasteful to birds and have different patterns of warning coloration. Birds learn to associate common color patterns with distastefulness, but are likely to attack butterflies with rare, unfamiliar phenotypes, such as hybrids. Researchers placed artificial butterflies, with wing patterns of two species and their F_1 hybrid, in a tropical forest, and scored the number that were damaged by attacking birds [60]. Those with hybrid color patterns were more frequently attacked (FIGURE 9.11).

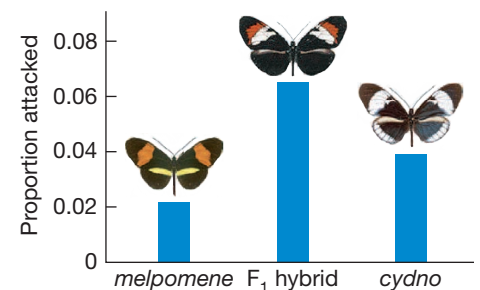


FIGURE 9.11 Model butterflies with the color pattern of the F_1 hybrid between *Heliconius melpomene* and *H. cydno* were attacked by birds significantly more frequently than those with the pattern of either parent. The low survival of hybrids is an example of postzygotic isolation caused by an extrinsic factor. (From [60].)

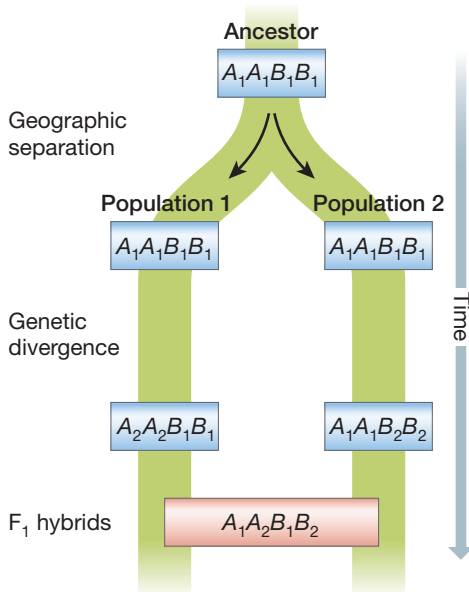


FIGURE 9.12 Dobzhansky-Muller incompatibilities (DMIs) can evolve when geographically separated populations become fixed for different alleles at two loci. (After [75].)

Postzygotic isolation is *intrinsic* if hybrids suffer high mortality, or are partially or entirely sterile, irrespective of environment. The causes of intrinsic postzygotic isolation and its genetic bases are diverse. Reduced hybrid viability is largely caused by incompatible interactions among genes from the two populations when they occur together in hybrids. Hybrid fertility may be reduced by incompatible genes or by differences in the number or structure of chromosomes. Bear in mind that the genetic differences that cause these effects may have evolved after prezygotic barriers, so we cannot assume that they were the cause of speciation.

Incompatible interactions between genes inherited from the two parents were postulated by Theodosius Dobzhansky in 1937 [21] and by Hermann Muller in 1942 [62], and are often referred to as **Dobzhansky-Muller incompatibilities (DMIs)**. The Dobzhansky-Muller hypothesis is clever because it explains how incompatibilities between populations can originate without ever producing incompatibilities within a population (**FIGURE 9.12**). Imagine that the ancestor of the two species had genotype $A_1A_1B_1B_1$. That species was then divided into two populations by a geographic barrier. In one population, allele A_2 spreads to fixation (perhaps because of adaptation to local conditions). This population is now $A_2A_2B_1B_1$. In the second population, allele B_2 spreads to fixation, so this population becomes $A_1A_1B_2B_2$. During this period, alleles A_2 and B_2 have never been in the same population, so there is no reason they should have been selected to function well together. If they are incompatible, hybrids between the two populations will have low fitness.

A simple example has been described for a cross between strains of the mouse-ear cress *Arabidopsis thaliana* from different regions [6]. Both strains have two paralogous loci (call them α and β), formed by duplication. In one strain, the α locus is nonfunctional, but the β locus is functional. The other strain has a functional α but a nonfunctional β . The F_1 offspring of a cross between the strains are viable, but in the F_2 generation, some recombinant offspring are homozygous for nonfunctional alleles of both α and β genes—a lethal combination.

DMIs between *Drosophila simulans* and *D. mauritiana* cause male F_1 hybrids to be sterile, while females are fertile. The genetics of the hybrid male sterility have been studied with laboratory crosses that produce different combinations of chromosome segments [13]. Two results emerge. The first is that many combinations of chromosomes from the two species reduce male fertility, showing that there are many DMIs throughout their genomes. The second is that male sterility is caused by interactions between the autosomes of *simulans* and the X chromosome of *mauritiana*. This reflects a general phenomenon called **Haldane's rule**: hybrid sterility or hybrid inviability is often limited to the heterogametic sex. (The heterogametic sex is the one with two different sex chromosomes, while the homogametic sex has two sex chromosomes of the same type.) In mammals and most insects, males are XY and thus are the heterogametic sex. In birds and butterflies, the situation is reversed: females have two different kinds of sex chromosomes. Thus male hybrids are frequently sterile in mammals (for example, mules), while female hybrids are frequently sterile in birds.

DMIs have many causes. Gene regulation can be anomalous due to a mismatch between *cis*- and *trans*-regulatory elements from the two species [11]. Intragenomic conflict (see Chapter 12) appears to be a common cause (see below) [18, 75]. DMIs can also be manifestations of cytonuclear incompatibility. For example, hybrids between different geographic populations of a marine copepod have reduced survival and fecundity if their mitochondria and nuclear genome come from different populations (**FIGURE 9.13**) [9].

Many sister species are distinguished by chromosome rearrangements: structural differences between the chromosomes (see Chapter 4). Two common

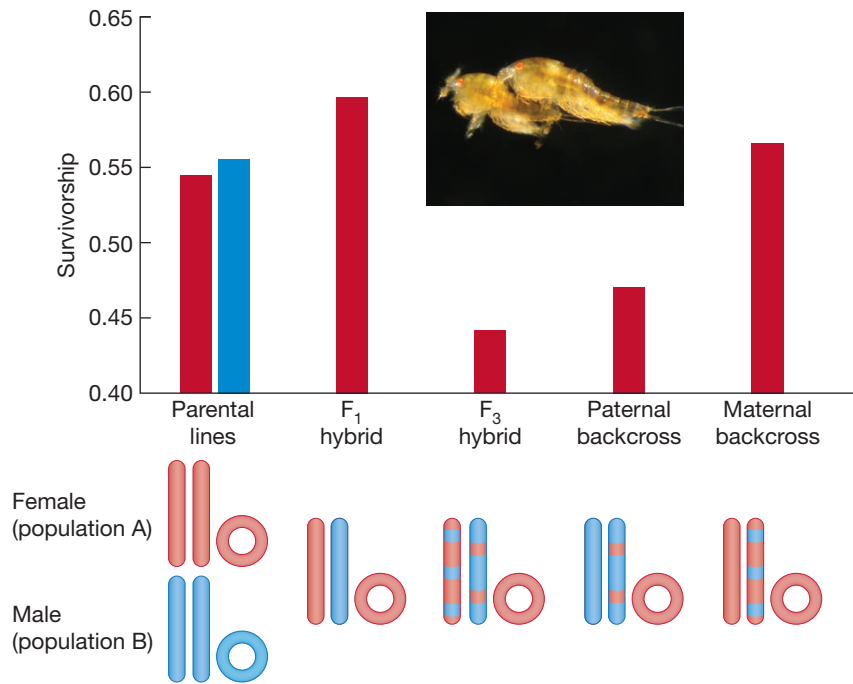


FIGURE 9.13 Crosses show that the low fitness of hybrids between populations of the copepod *Tigriopus californicus* is caused by a genetic mismatch between mitochondrial and nuclear genes. Maternally inherited mitochondria (circles) and nuclear chromosomes inherited from both parents (rods) of populations A and B are colored red and blue, respectively. Crosses produce F₁ hybrids with population A mitochondria. These F₁ offspring have slightly higher survival, showing “hybrid vigor.” Crosses then produce F₂ and F₃ hybrids, with recombined nuclear genes. The paternal backcross is produced by mating F₃ females with population B males. These offspring have low fitness, because most of the nuclear genes come from population B and are mismatched to the mitochondrial genes from population A. In contrast, offspring of the maternal backcross, in which most of the nuclear genes come from the same population as the mitochondria, have normal, high survival. (After [9].)

rearrangements are **inversions** and **reciprocal translocations** (see p. 90). Especially in the case of translocations, heterozygotes have reduced fertility compared with homozygotes for either the original or the derived (new) arrangement. For this reason, populations with different chromosome arrangements are nearly or entirely monomorphic, and may form narrow hybrid zones where one “chromosome race” meets and interbreeds with another (**FIGURE 9.14**). The fertility of heterozygotes for chromosome rearrangements may be low either because the rearrangements carry different alleles that create Dobzhansky-Muller incompatibilities, or because of mispairing of chromosomes in meiosis produces gametes that lack certain chromosome regions.

How fast does reproductive isolation evolve?

The time required for reproductive isolation to become strong, after it has started to evolve, varies greatly. The origin of a new species by polyploidy, which is especially common in plants, requires only one or two generations (see p. 232). If

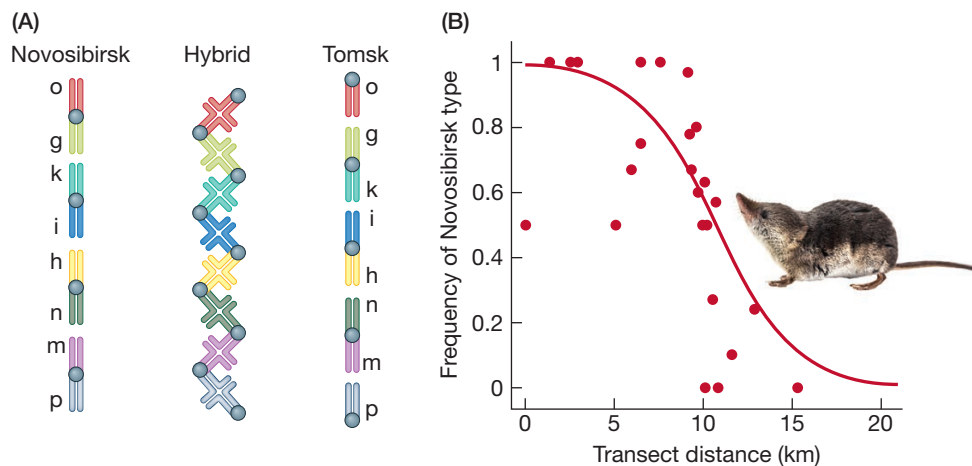
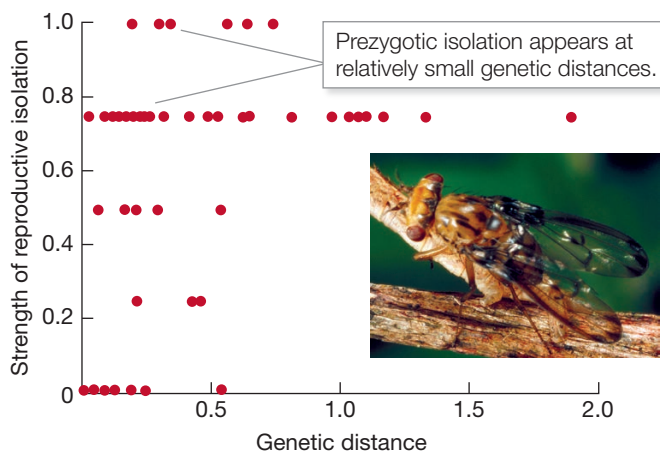


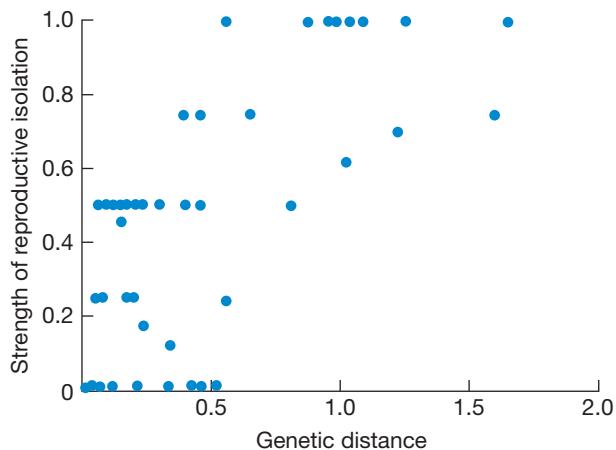
FIGURE 9.14 Two “chromosome races” of the common shrew (*Sorex araneus*) form a very narrow hybrid zone in Siberia. (A) The Novosibirsk and Tomsk races differ by the fusion of some single-armed chromosomes (e.g., o and p in Tomsk) into double-armed chromosomes (e.g., o and g in Novosibirsk). In meiosis in hybrids, the multiple rearrangements cause a chain of nine chromosomes to form, and irregular segregation produces many unbalanced gametes and low fertility. (B) A transect from Novosibirsk to Tomsk shows a cline in the frequency of the Novosibirsk chromosome arrangement less than 9 km wide. The chromosome configuration of either race cannot increase within populations of the other race, probably because meiosis in F₁ hybrids produces gametes that lack some chromosomal regions. (A after [73]; B after [74].)

(A) *Drosophila*

Prezygotic isolation



Postzygotic isolation



(B) *Etheostoma*

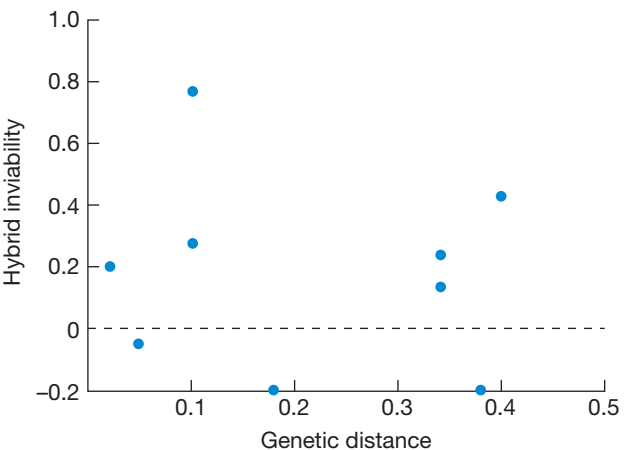
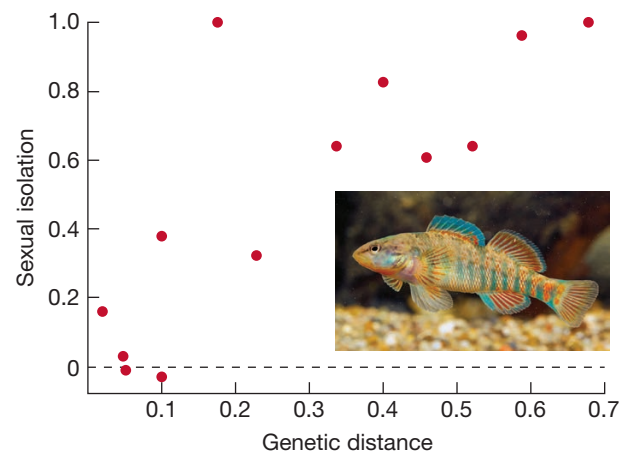


FIGURE 9.15 Prezygotic isolation evolves faster than postzygotic isolation in flies and fishes. (A) The strength of prezygotic and postzygotic reproductive isolation between pairs of populations and species of *Drosophila* increases with the amount of time since the lineages split. The time is estimated by the genetic distance between each pair. The strength of prezygotic isolation was measured by observing mating between flies in the laboratory. The strength of postzygotic isolation was measured by survival and fertility of hybrid individuals. Comparison of the upper

left part of the two graphs reveals that strong prezygotic isolation evolves shortly after isolation (at small genetic distances), while strong postzygotic isolation evolves only later. (B) Similar patterns are seen in a genus of freshwater fishes, the darters (*Etheostoma*). Thirteen pairs of allopatric species were tested for both sexual isolation and the survival of artificially produced hybrids. For both indices, a value of 0 indicates that the pairs are no more isolated than conspecific individuals, and a value of 1 indicates complete reproductive isolation. (A after [14]; B after [59].)

450-plus species of cichlid fishes evolved from 5 ancestral species in Lake Victoria in just 15,000 years (see opening of this chapter), the average time between speciation events was less than 2000 years, which is astonishingly rapid. Molecular clocks (see Chapter 7) can be used to estimate the time back to the most recent common ancestor, giving us the age of their speciation. Based on this approach, sympatric sister species of *Drosophila* are estimated to have taken about 200,000 years to evolve, while it requires 1.1–2.7 million years for allopatric populations to evolve full reproductive isolation [15]. Some populations of birds that have been diverging for 1.5–3 million years form hybrid zones, showing that it takes more time for birds than flies to evolve strong reproductive isolation [106].

In many groups of organisms, prezygotic isolation evolves considerably faster than intrinsic postzygotic isolation (FIGURE 9.15). Consequently, closely related species are often fully interfertile: many species and genera of birds, even after more than 5 million years of divergence, can form fully viable, fertile hybrids when crossed [76]. In these cases (which may be the rule in many kinds of organisms),

postzygotic isolation probably plays a minor role in speciation. It may, however, affect the further evolution of prezygotic isolation (see p. 230), and it may help keep species separate, because prezygotic barriers such as ecological or sexual isolation may not evolve to completion, or can become weaker if habitats change [87]. For example, increasing turbidity in Lake Victoria interfered with female cichlids' ability to see differences in male coloration that are the basis of sexual isolation between some closely related species. The result is that species that were previously well isolated are now hybridizing [96]. In contrast, strong postzygotic isolation, such as complete hybrid sterility, is probably irreversible, and can make species permanent.

The Causes of Speciation

Speciation is the evolution of reproductive isolating barriers. But because these barriers decrease the chance that some individuals mate or that their offspring survive, it might seem paradoxical that they could ever evolve.

The solution to this conundrum is that speciation often starts with a geographic barrier (such as a mountain range) that separates two populations of the same species. Over time, the populations evolve genetic and phenotypic differences, perhaps as they adapt to different ecological conditions. At this stage, there is no reason that genetic differences between the populations, or traits such as mating behavior, should be compatible, because the genes in the two populations are prevented from mixing by the geographic barrier. Sometimes those differences cause prezygotic or postzygotic isolation between the populations if they come back into contact (for example, if the mountain range erodes or if colonists disperse across it). If reproductive isolation is sufficiently complete, two species have evolved from one by the process of **allopatric speciation**. (Remember, we defined reproductive isolation as based on biological differences that reduce gene exchange, not extrinsic barriers such as mountain ranges.)

This scenario illustrates a key point: to initiate speciation, something is needed to restrict free interbreeding between two diverging populations, since interbreeding tends to erase their emerging genetic differences. Most often, that restriction results from geographic separation of the populations, although other mechanisms can have this effect.

We now turn to the question of what causes the evolution of genetic and phenotypic differences between geographically separated populations that result in reproductive isolation. That is, what are the causes of speciation?

ECOLOGICAL SPECIATION The two monkeyflower species discussed earlier (see Figure 9.7) provide a vivid example of how reproductive isolation can result when natural selection acts differently on two populations [91]. Based on phylogenetic reconstruction of ancestral characteristics in the genus, it is likely that the ancestor of these species resembled *Mimulus lewisii* (see Figure 9.7A): it was bee-pollinated and occupied high elevations. The population that gave rise to *M. cardinalis* colonized lower elevations, where natural selection favored flower traits that attract hummingbirds: red pigments, abundant nectar, and extension of the petals to form a long, tubular corolla that excludes bees but allows hummingbirds to reach the nectar (see Figure 9.7B). Those changes to the elevational distribution and flowers had the effect of strongly decreasing the exchange of pollen (and genes) with the ancestral population, giving rise to the new species.

This scenario is a plausible reconstruction of past events. Biologists have also observed the evolution of reproductive isolation by selection in the laboratory. **BOX 9B** describes an experiment in which laboratory populations of *Drosophila melanogaster* were selected for adaptation to two different environments. In only about 20 generations, the divergently selected subpopulations became substantially reproductively isolated.

BOX 9B

Speciation in the Lab

Can different regimes of natural selection cause populations of a species to become different species? Darwin and many later evolutionary biologists have supposed that this is how speciation usually happens. Indeed, most closely related species have different adaptations to their ecological circumstances (for example, they often are adapted to slightly different habitats or diets), and of course they are reproductively isolated. But that does not provide evidence that the genetic changes underlying their ecological adaptations caused the reproductive isolation.

One way of obtaining relevant evidence is to use experimental evolution. In this approach, we expose a laboratory population to a simplified version of the conditions we suspect might occur in nature. The results determine if real organisms can in principle speciate because of different ecological selection pressures. We can also gain other key insights, for example how long the process might take.

Among many such experiments is one by Diane Dodd [21], who used eight laboratory populations of *Drosophila pseudoobscura*, all of which were founded by flies collected in a single locality in Utah. For 1 year (about 20 generations), four of the populations were reared on each of two larval food media, one based on starch (*st*) and the other on maltose (*ma*). Both media were stressful: Dodd reported that “it initially took several months for the populations to become fully established and healthy.” Thus these treat-

ments provided conditions for adaptation to the different diets to occur by natural selection. (It was natural selection, not artificial selection. In artificial selection, the investigator would decide which flies reproduce and which do not. Dodd didn’t do that. Instead, she simply put the flies into a stressful environment and let selection take its course.)

After a year, Dodd reared flies from all eight populations on standard *Drosophila* food for one generation (to eliminate any maternal effects of starch or maltose). She then put virgin females and males from a pair of populations together in an observation chamber and recorded how many of each of the possible matings occurred. For instance, in one combination of *st* and *ma* populations, two kinds of “homogamic” matings (female *st* × male *st*, female *ma* × male *ma*) and two “heterogamic” matings (female *st* × male *ma*, female *ma* × male *st*) might occur. Each of the 16 possible pairs of starch-adapted and maltose-adapted populations was tested in this way. In order to be sure that any reproductive isolation could be attributed to the divergent selection, and not just genetic drift in isolated populations, Dodd also counted matings between pairs of populations that had been subjected to the same stressful diet. For every pair of populations, an index of sexual isolation was calculated that ranged from 0, if the proportion of different-population matings equaled the proportion of same-population matings, to 1.0 if no different-population matings

The monkeyflowers and the *Drosophila* experiment illustrate how reproductive isolation can evolve as a side effect of adaptation to different ecological circumstances, a process called **ecological speciation** [64, 93]. A key point is that the RIBs evolve by pleiotropy (see Chapter 4). There was no direct natural selection for isolation between the populations. Rather, selection acted on other traits that happened to cause isolation. (Recall the distinction between “selection for” and “selection of” features, in Chapter 3.) Although speciation, one of the most important elements of evolution, is commonly a consequence of adaptive changes in organisms’ characteristics, it is typically not an adaptation itself.

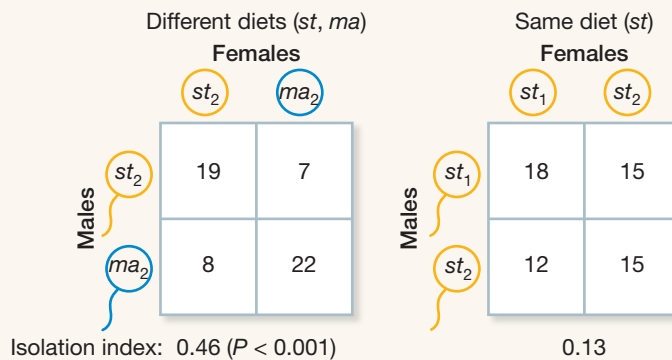
SPECIATION BY GENETIC CONFLICT Another powerful cause of the evolution of reproductive isolation is **genetic conflict**, which occurs when an allele increases its own transmission to the detriment of other alleles at the same or other loci (see Chapter 12). Many mutations have been found that transmit more copies of themselves to the next generation not by increasing survival or reproduction, but by violating the rules of inheritance. They are transmitted to more than 50 percent of the gametes (a process called **segregation distortion**). These mutations increase in frequency in a population even though they often reduce

BOX 9B

Speciation in the Lab (continued)

occurred. (Incidentally, for these tests Dodd clipped a wing tip on flies from one of the two experimental populations, in order to distinguish them. This procedure did not affect the results.)

Here are the numbers of matings for 1 of the 16 pairs of populations adapted to different diets, and 1 of the 16 pairs adapted to the same diet:



Females of the st and ma populations, adapted to different diets, were more likely to accept males adapted to the same diet as themselves. In all 16 combinations of different-diet populations, there was a tendency for females to show same-diet preference, and this was statistically significant in 11 combinations. (The notation $P < 0.001$ means that the probability is less than 1 in 1000 that the correlation be-

tween mating and rearing environment could have occurred by chance.) But in none of the pairs of populations adapted to the same diet was there a statistically significant excess of same-population matings.

The sexual isolation index value of 0.46 suggests that in a mere 20 or so generations, these divergently selected laboratory populations had progressed about halfway toward full sexual isolation—in which case speciation would have been completed in the laboratory! This is astonishingly fast, especially in the context of evidence on how long it takes for speciation to occur in nature (see p. 226).

What caused the populations to evolve partial sexual isolation? One possible answer is pleiotropy: some of the same genes that enhance adaptation to starch or maltose might also affect female preference and some feature of males that enables females to distinguish them. Or perhaps the strong selection for alleles that enhance adaptation to the novel diets carried along alleles at closely linked genes that affect male characteristics and female responses to those characteristics.

Dodd did not do further research on these possibilities, and in the 1980s it would not have been possible to identify and obtain the sequences of the relevant genes. That would be a much easier task today. Dodd's experiment is waiting for someone to repeat it and do the genetic detective work.

fertility. Selection therefore favors mutations at other loci that restore full fertility by disabling the segregation distortion caused by the "selfish" mutation.

When this conflict between distorter and a restorer has played out in one population but not another, the populations may be genetically incompatible. This is the basis for strong postzygotic isolation between populations of *Drosophila pseudoobscura* in North America and in Bogotá, Colombia: hybrid males are almost completely sterile [71]. Sterility is the result of a mutation at a locus (*Overdrive*) that reduces male fertility, but that spreads by segregation distortion through the Bogotá population. This population has restorer alleles at other loci that maintain male fertility, but restoration is inadequate in hybrid males. Genetic conflict seems to be an important cause of Dobzhansky-Muller incompatibilities in *Drosophila* and perhaps other groups of organisms. A similar conflict sometimes occurs between nuclear and mitochondrial or chloroplast genes, as in the copepod example described earlier (see Figure 9.13).

Earlier we saw that different species of abalones are reproductively isolated because proteins on the outside of their eggs and sperm have diverged to the point where they do not bind to one another. Divergence may have been caused by sexual conflict: changes in the egg surface that slow down sperm entry are

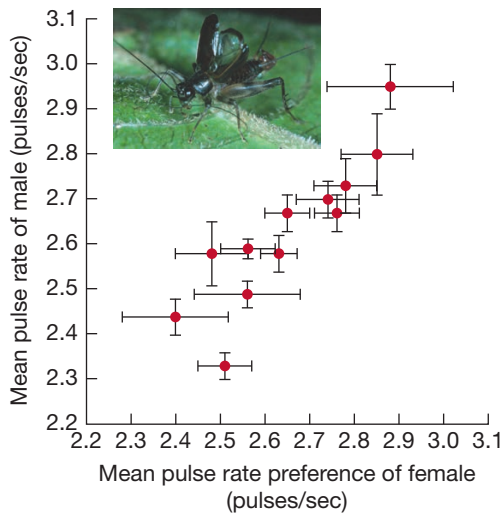


FIGURE 9.16 Evolution of sexual isolation by sexual selection. The pulse rate of the mating call of male crickets (*Laupala cerasina*) and the pulse rate preferred by females both vary among local populations. These differences are genetically based. The confidence intervals around each point show that the preference ranges of females of the most widely different populations would not include the most divergent males. (After [33].)

advantageous because fertilization by more than one sperm kills the egg. Any such changes in the egg will impose selection for sperm that can beat their competitors by penetrating more quickly [99].

SPECIATION BY SEXUAL SELECTION In many groups of rapidly speciating animals and plants, species differ more in their secondary sexual traits,¹ such as male coloration or vocalization, than in ecologically important traits (see Figure 9.9). In many cases, one sex (let's suppose the female) chooses mates based on variation in these traits. Females impose strong sexual selection, which can drive the rapid evolution of male secondary sexual traits (see Chapter 10). Species that differ in sexually selected male features also commonly differ in female preference, so females recognize and mate preferentially with males of their own species. These patterns suggest that divergent sexual selection can cause rapid evolution of prezygotic isolation between populations [88]. Certain groups of animals, such as cichlid fishes and hummingbirds, have indeed speciated rapidly and show strong sexual selection. Recent phylogenetic analyses of birds suggest that male coloration patterns associated both with sexual selection and species recognition evolve fastest in lineages with high speciation rates [94].

Studies of closely related populations and species provide more direct evidence that sexual selection may cause speciation. For example, male calls and female preferences covary among populations of a Hawaiian cricket (*Laupala cerasina*), to the point that females hardly respond to the calls of the most different population (**FIGURE 9.16**) [33]. Sexual isolation appears to be the sole basis of reproductive isolation between some ecologically indistinguishable species of freshwater fishes called darters (see Figure 9.15B) [52]. Why then does sexual selection vary among populations? In Chapter 10 we will consider some of the factors at work. These include direct benefits to mate preferences, selection acting on pleiotropic effects of preference genes, preferences for mates with “good genes,” and ecological factors that make different courtship signals more effective in different environments.

REINFORCEMENT OF REPRODUCTIVE ISOLATION So far, we have discussed how speciation can result as a side effect of divergent selection. In some cases, natural selection can also directly favor the evolution of prezygotic isolation. Consider two populations that have already evolved some degree of isolation so that hybrids have lower survival or fertility. A female that chooses a male from her own population will leave more descendants than one that makes the mistake of mating with a male from the other population. This creates a selective advantage to an allele for a mating preference that increases the chance of mating within rather than between populations. A “discrimination” allele will be transmitted to more progeny, on average, than a “random-mating” allele.

The evolution of stronger prezygotic isolation because of selection against low-fitness hybrids is called **reinforcement**. Not all types of isolating mechanisms can evolve this way. Alleles that strengthen *prezygotic* isolation gain an advantage because individuals with them have higher fitness than do those that hybridize. But stronger *postzygotic* isolation usually cannot evolve by natural selection. An allele that lowers hybrid fitness cannot increase in frequency, for that would be the antithesis of natural selection. (Exceptions are in organisms such as plants and mammals, in which embryos compete for the mother's nutrients. It can be advantageous for a mother to abort hybrid embryos and allocate resources to nonhybrid

¹Secondary sexual traits are those that differ between the sexes, other than the gonads and reproductive structures.

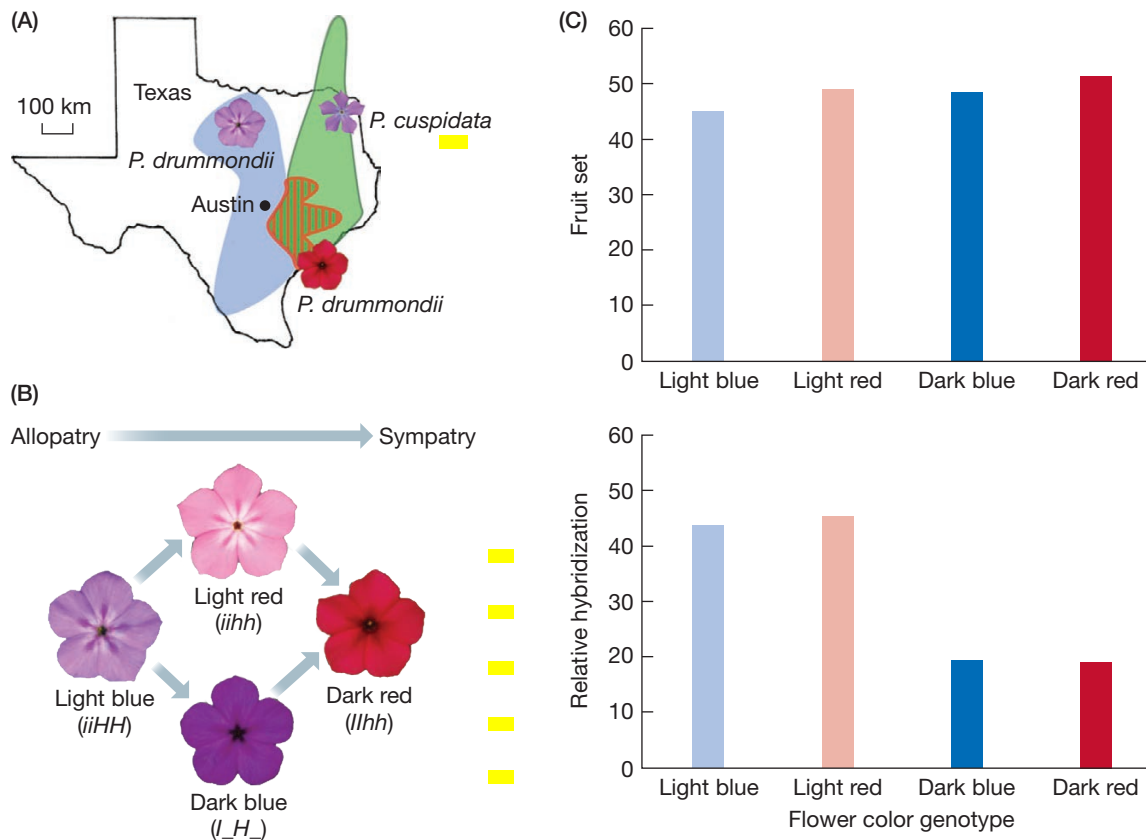


FIGURE 9.17 Reinforcement of reproductive isolation by flower color in *Phlox*. (A) The geographic distributions of *P. cuspidata* and *P. drummondii* overlap in Texas. Allopatric populations of both species are light blue, but populations of *P. drummondii* are dark red where the species is sympatric. (B) The flower color difference in *P. drummondii* is based on two loci. (C) Results of common-garden field experiments, in which all four color types of *P. drummondii* were grown together with *P. cuspidata*. Both parental types (light blue and dark red) and hybrid genotypes with light red and dark blue flowers have equal fruit production (top graph), but differ in the proportion of their offspring that are hybrids with *P. cuspidata* (bottom graph). (A and B from [37]; C after [37].)

offspring that are more likely to pass on her genes [12].) This is one reason why the distinction between prezygotic and postzygotic mechanisms is important: prezygotic mechanisms can evolve by reinforcement, but postzygotic mechanisms generally cannot.

Wildflowers in the genus *Phlox* provide a clear example of reinforcement [37]. Allopatric populations of the two species *Phlox drummondii* and *P. cuspidata* both have light blue flowers (FIGURE 9.17). Where their ranges overlap, however, *P. drummondii* has evolved dark red flowers, a difference in color caused by changes at two loci. Because the fertility of hybrids is up to 90 percent lower than that of non-hybrids, the difference in color is strongly favored by selection: pollinators move less pollen between flowers that have different colors, so *P. drummondii* produces fewer low-fitness hybrids when it has dark red flowers rather than light blue flowers in the zone of sympatry.

Selection for reinforcement can occur only when two species continue to interbreed after some postzygotic isolation (reduced fitness of hybrids) has already evolved between them. If reinforcement is common, we would expect sympatric pairs of species (which could potentially hybridize) to show greater prezygotic isolation than allopatric pairs of species (which have no chance of hybridizing).

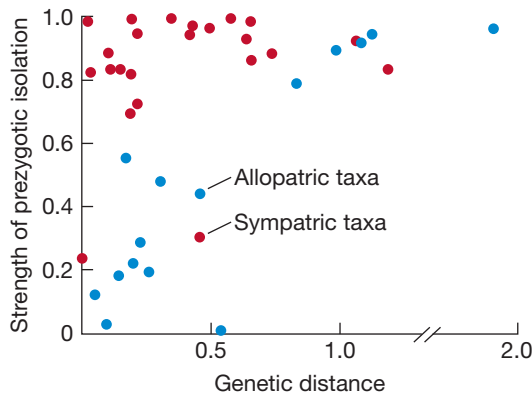


FIGURE 9.18 In *Drosophila*, the strength of prezygotic isolation increases more rapidly between sympatric pairs of species (red dots) than it does between allopatric pairs (blue dots). The genetic distance between members of a pair is an index of the time since divergence began. At small genetic distances, many sympatric pairs show strong isolation, but allopatric pairs do not. (After [14].)

Data from *Drosophila* show exactly the expected pattern. In **FIGURE 9.18**, the strength of prezygotic isolation between a pair of populations or species is plotted against the genetic difference (or genetic “distance,” based on molecular differences) between them. Prezygotic isolation here refers to behavioral isolation when females’ choice between males of both species was observed in laboratory tests. The genetic distance serves as a molecular clock, indicating time since the species diverged from their common ancestor. Sympatric pairs of species show strong prezygotic isolation at lower genetic distances than do allopatric pairs, meaning they evolved mating discrimination faster. This pattern is what we expect if the sympatric pairs tended to hybridize shortly after speciation, and reinforcement then strengthened their prezygotic isolation. Further analysis reveals additional support for the role of reinforcement. Hybridization between some pairs of sympatric species is asymmetric: the offspring from a cross between a female of species A and a male of species B have lower fitness than those from the reciprocal cross (female B \times male A). In these cases, sexual isolation is stronger in the female-male combination that produces less fit hybrids, as we predict from the hypothesis of reinforcement [108].

SPECIATION BY POLYPLOIDY When a diploid species’ entire genome is doubled (see Chapter 4), the result is a tetraploid that has four copies of every chromosome. Tetraploids originate by the union of two “unreduced” gametes—both carrying a full diploid set of chromosomes—that

are formed when chromosomes occasionally fail to segregate in meiosis. The polyploid offspring is *autopolyploid* if both unreduced gametes come from the same diploid species, and *allopolyploid* if they come from different diploid species. If similar events happen in tetraploid species, offspring with even more sets of chromosomes (e.g., eight in octoploids) result. The increased number of gene copies in polyploids changes the expression (e.g., amount of gene product) of many genes, and alters many phenotypic traits [50, 67].

Tetraploids typically have complete reproductive isolation from their diploid ancestors, and so are distinct biological species that have arisen in one step [79]. That is because hybrids between a diploid and a tetraploid are triploid: they have one set of chromosomes from the diploid parent and two from the tetraploid parent (in which four homologous chromosomes generally segregate two by two in meiosis). Triploids are largely sterile [38], because their gametes are unbalanced: they have one copy of certain chromosomes and two copies of other chromosomes. Genome doubling is a large mutational event: one of the very rare situations in which mutations of large effect make important contributions to evolution, in this case the origin of new species.

Speciation by polyploidy is rare in animals, but it is quite common in some groups of plants. It accounts for about 15 percent of speciation events in flowering plants [107], and all plants have a polyploid ancestor somewhere in their evolutionary past [67]. Speciation by polyploidy has occurred even very recently. For example, hybridization among three species of goatsbeards (*Tragopogon*) generated new allopolyploid species within the last several centuries, after their accidental introduction to North America from Europe (**FIGURE 9.19**).

How can a new tetraploid build up a population? There is a serious obstacle. The tetraploid species starts out with just one or a few individuals, so often the diploid ancestor is more abundant in its habitat. This can cause the tetraploids to hybridize most often with the diploids, producing triploid offspring with low fitness and pushing the tetraploid toward extinction. A new tetraploid might increase if hybridization were reduced by self-fertilization, vegetative propagation, higher fitness than the diploid, or habitat segregation from the diploid [27, 84]. Many

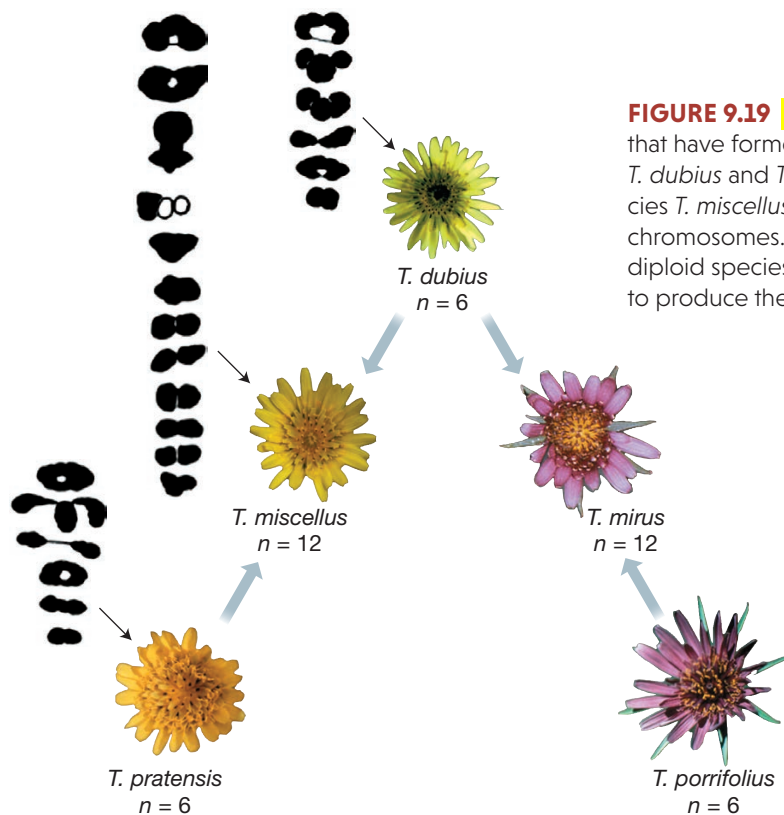


FIGURE 9.19 Several species of goatsbeards (*Tragopogon*) are tetraploids that have formed by hybridization (allotetraploids). The diploid species *T. dubius* and *T. pratensis* hybridized and produced the tetraploid species *T. miscellus*. Next to the pictures of the flowers are drawings of their chromosomes. The tetraploid has twice as many chromosomes as the two diploid species. *T. dubius* has also hybridized with the diploid *T. porrifolius* to produce the tetraploid *T. mirus*. (After [68, 72].)

tetraploid taxa do indeed reproduce by selfing or vegetative propagation, and most differ from their diploid progenitors in habitat and distribution, and so would be segregated from them. The phenotypic differences that are an immediate effect of chromosome doubling may cause such separation. In California, tetraploids and hexaploids of the yarrow *Achillea borealis* grow in wetter and drier habitats, respectively. Justin Ramsey planted seedlings of both forms in dry dunes, as well as “neohexaploids” that had originated de novo from tetraploid parents that he grew [78]. The neohexaploids survived better and flowered earlier than the tetraploids (FIGURE 9.20), showing that they would be partly isolated from the tetraploids, by habitat and flowering time, immediately upon their origin.

HYBRID SPECIATION Interbreeding between populations usually opposes divergence and so makes speciation less likely. Occasionally, however, hybridization generates a new species without help from polyploidy [1]. For example, three species of sunflowers have originated from independent hybridization events

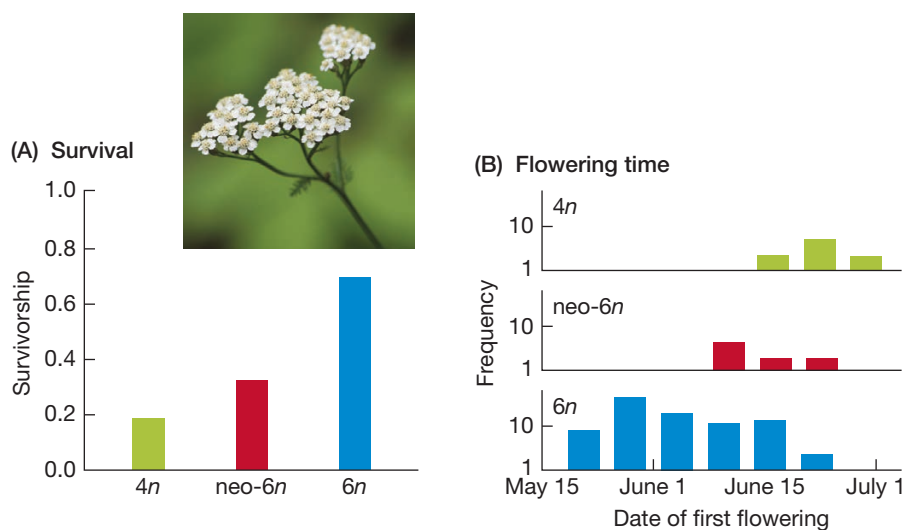


FIGURE 9.20 Differences between a newly formed polyploid and its ancestor may confer ecological differences that could reduce the opportunity for crossing between them. Survival (A) and flowering time (B) of a newly originated hexaploid (neo-6n) yarrow (*Achillea borealis*), planted in a dry dune, were intermediate between those of its tetraploid parent (4n) and an existing hexaploid (6n) species. Increasing the chromosome number immediately changes these characteristics, but the wild hexaploid (6n) differs even more from the tetraploid ancestor (4n), so the wild hexaploid must have undergone some additional evolutionary change. (After [78].)

between two parental species, *Helianthus annuus* and *H. petiolaris* (see Figure 2.11) [81]. All have the same number of chromosomes. The hybrid species live in drier or saltier habitats than the parents and are genetically incompatible with them. The combination of spatial separation, genetic incompatibilities, and perhaps other mechanisms effectively isolates the hybrid species from their parents.

DNA studies show that all three hybrid species have arisen from the same two parental species, but that they have different combinations of parental genes. The origin of the hybrids has also been confirmed experimentally, by crossing the parental species. Their F_2 hybrids show some of the same distinctive adaptive features as the wild hybrid species [82].

SPECIATION BY RANDOM GENETIC DRIFT Some closely related species differ by chromosomal rearrangements that contribute to postzygotic isolation because of low fertility of chromosome heterozygotes. In the sunflowers just discussed, about half of the postzygotic barrier between *H. annuus* and *H. petiolaris* is caused by underdominant chromosomal rearrangements [36, 83]. How these isolating mechanisms evolve is puzzling, because underdominant mutations are selected against when they first appear (see Chapter 5). How, then, can these chromosome rearrangements increase and become fixed in one of the two sister species?

One possible answer is random genetic drift. If the population size is so small that genetic drift is stronger than selection, there is a chance that the new rearrangement will increase in frequency even if heterozygotes have decreased fitness. Several factors, including self-fertilization and large fluctuations in population size, make this more probable. Drift is unlikely to establish individual rearrangements that cause very strong postzygotic isolation, because the force of selection against them will be overwhelming.

But even a rearrangement that makes only a small contribution to reproductive isolation at first may later reduce gene exchange with other populations of the other species. For example, heterozygous inversions suppress recombination (see Chapter 4). If a species becomes fixed for a new chromosomal inversion, either by drift or some other mechanism, hybrids with other populations of the species will be heterozygous for the inversion, and genes in that chromosome region will not introgress between the populations. Thus, genetic differences between the populations accumulate more rapidly in the inverted region than in other parts of the genome [63].

One hypothesis for how random genetic drift might trigger the origin of new species is called **founder effect** or **peripatric speciation**. Drift can be particularly strong when a new population is founded by a small number of individuals (see Chapter 7). Under this hypothesis, proposed by Ernst Mayr [56, 58], drift in a new population, founded by a few individuals, fixes rare alleles at certain loci. Alleles at other loci that increase fitness by interacting favorably with these newly fixed alleles increase, resulting in a new combination of genes that may be genetically incompatible with the parent population from which the colony was derived. Mayr suggested that founder effect speciation is an important way that new species arise at the periphery of species ranges, and he offered potential examples from island populations of birds (**FIGURE 9.21**). Founder effect speciation is controversial both for theoretical and empirical reasons [2, 54, 97].

A possible example of this idea is the cytonuclear incompatibility between populations of the copepod described in Figure 9.13. In that case, a deleterious mutant mitochondrial genotype may have been fixed by genetic drift, followed by selection for nuclear alleles that counteract the harmful mitochondrial genotype and restore high fitness. Several investigators have tested the idea that drift can cause the evolution of reproductive isolation by passing laboratory populations of fruit flies through bottlenecks (see Chapter 7), then measuring reproductive isolation

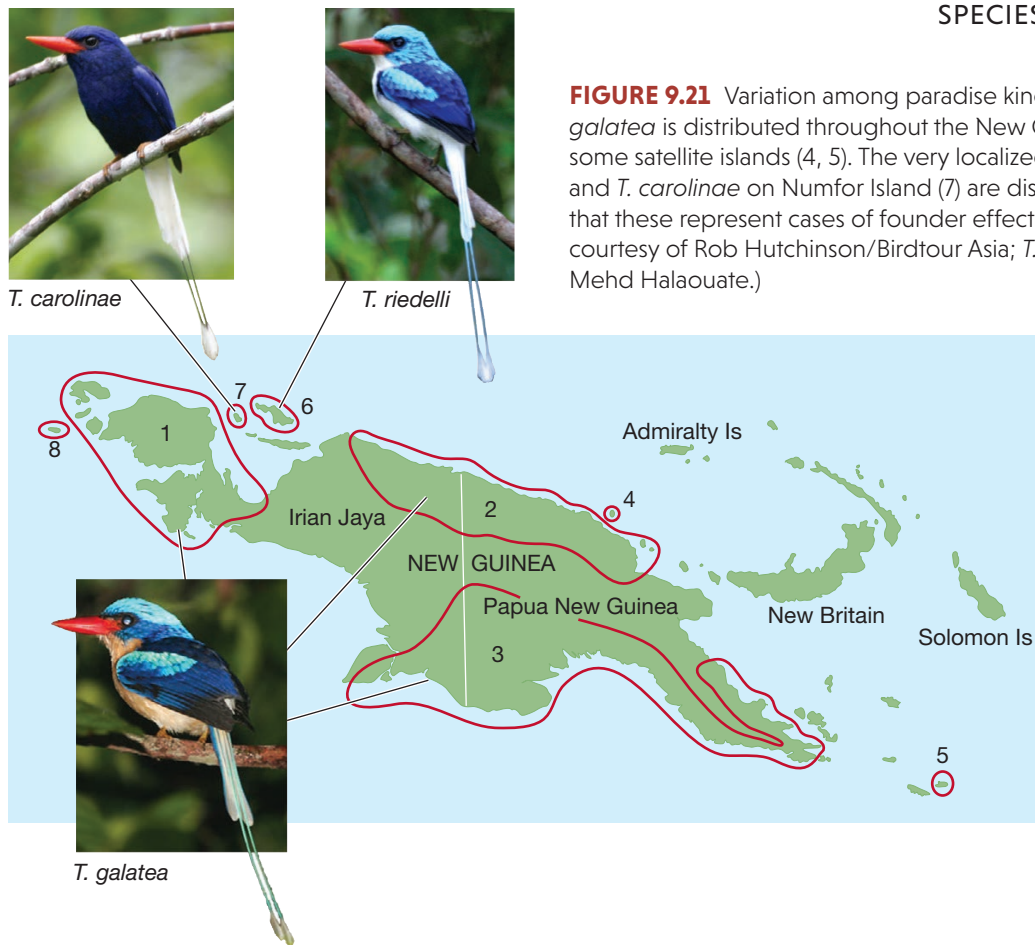


FIGURE 9.21 Variation among paradise kingfishers in New Guinea. *Tanysiptera galatea* is distributed throughout the New Guinea lowlands (regions 1, 2, 3) and some satellite islands (4, 5). The very localized forms *T. riedelii* on Biak Island (6) and *T. carolinae* on Numfor Island (7) are distinct species. Mayr [56] proposed that these represent cases of founder effect speciation. (*T. galatea* photo courtesy of Rob Hutchinson/Birdtour Asia; *T. riedelii* and *T. carolinae* courtesy of Mehd Halaouate.)

several generations later [31, 54]. Typically a few of the replicate populations display sexual isolation from the parent population, although the change is often temporary. There is some disagreement about whether or not to view these results as support for founder effect speciation [15, 101].

The Geography of Speciation

A critical issue in understanding speciation is how the level of gene flow is initially reduced between two populations when they first start to diverge. This is key because populations cannot diverge, and evolve reproductive isolation, if gene flow is high enough to counteract divergence by selection or genetic drift.

The most common way for speciation to begin is with the appearance of a geographic barrier that partly or completely blocks genetic exchange between two populations (FIGURE 9.22) [15, 57]. This is allopatric speciation. In other cases, speciation occurs with little or no help from a geographic barrier. The most extreme case is when a single population splits into two reproductively isolated populations while living together, a process called **sympatric speciation**. An intermediate between those two situations is **parapatric speciation**, in which neighboring populations of a single species that exchange genes nevertheless diverge into two species. The critical difference among these situations is that sympatric speciation and parapatric speciation involve **speciation with gene flow**, while allopatric speciation does not. The following sections look into the details of allopatric speciation and speciation with gene flow.

Allopatric speciation

Allopatric speciation is *the evolution of genetic barriers between populations that are geographically separated* by a physical barrier (for example, a mountain range). Allopatry is defined by a severe reduction of movement of individuals or their

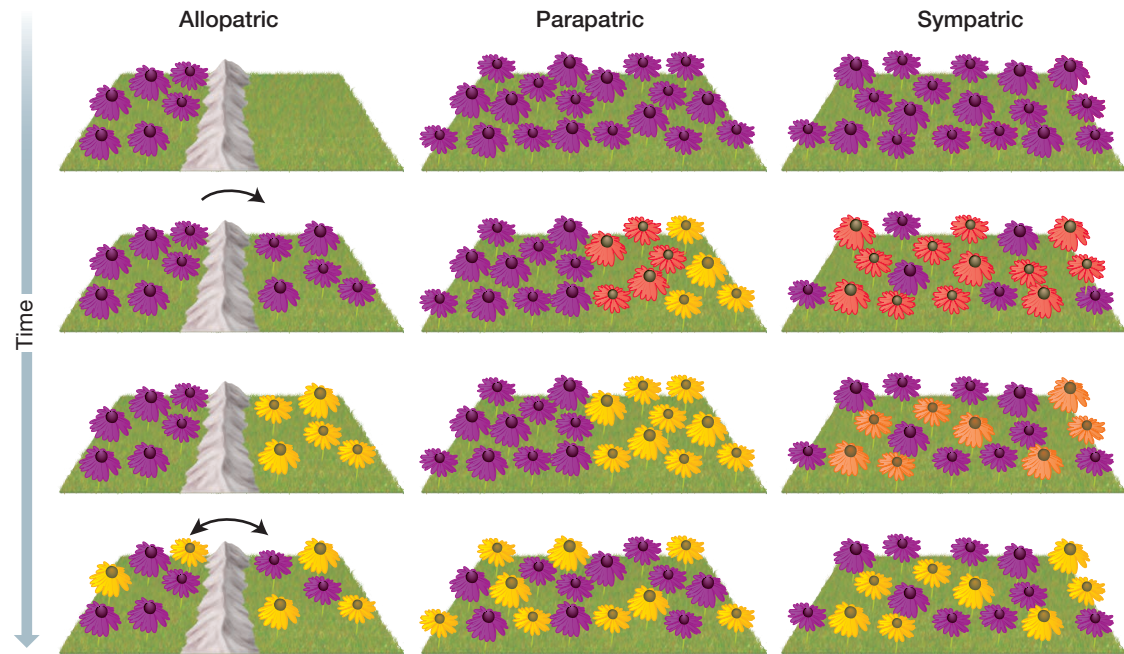


FIGURE 9.22 Schematic showing three types of speciation. In allopatric speciation, populations diverge (shown as increasing difference in color) while separated by a geographic barrier (such as a mountain range). In this drawing, an allopatric population is established by colonization. When the two populations have become so different that reproductive isolation has evolved, the two can coexist without interbreeding even if each form disperses into the range inhabited by the other (shown by the double-headed arrow). In parapatric speciation, neighboring populations diverge while still exchanging genes. In sympatric speciation, two new species emerge from a single ancestor without any geographic isolation.

gametes, not by geographic distance. In species that disperse little or are faithful to one habitat, populations may be “microgeographically” isolated (for example, among patches of favorable habitat along a lakeshore).

Allopatric populations can originate in two ways. One is **vicariance**, which is when a barrier appears and divides a population that was occupying a larger region. When the Isthmus of Panama rose out of the ocean several million years ago, it divided many marine species into Caribbean and Pacific populations. Since then, these populations have evolved into distinct species [44, 49]. Allopatric populations also originate by **dispersal**, when individuals from one population colonize another region. Speciation by dispersal has happened innumerable times when oceanic islands have been colonized from continental populations.

From paleontological and genetic studies (see Chapters 8 and 18), we know that species’ geographic ranges change over time, and that populations may become separated and later rejoined. If sufficiently strong isolating barriers have evolved during the period of allopatry, the populations may become sympatric without exchanging genes. Many sister species that today are sympatric have speciated allopatrically and then expanded their ranges. This means that *current sympatry, in itself, is not evidence that speciation occurred sympatrically*.

Many species show partial reproductive isolation among geographic populations. For example, when males and females from different populations of dusky salamanders (*Desmognathus ochrophaeus*) from various localities in the eastern United States are placed together, the level of sexual isolation among them varies. The more geographically distant the populations, the less likely they are to mate (**FIGURE 9.23**) [102]. Similarly, sexual isolation has been shown among allopatric species of darters

that occupy different river systems (see Figure 9.15B). Often, allopatric speciation can be related to the geological history of barriers that emerged between populations of a widespread ancestral species, as with the Isthmus of Panama.

Species on islands provide abundant evidence of allopatric speciation. For example, no pairs of sister species of birds occur together on any isolated island smaller than 10,000 km². This observation implies that speciation in birds does not occur on land masses that are too small to provide geographic isolation between populations [16]. A similar pattern is found in many other taxa [43]. As expected, taxa in which gene flow is high (such as bats) have speciated only on very large islands, while taxa in which gene flow is very limited (such as snails) have speciated on small islands (FIGURE 9.24).

The role of geographic isolation on islands is obvious, but what kinds of barriers could have produced the great numbers of species that are found on continents? Geographic distributions may be fragmented if populations maintain dependence on specific environmental conditions, such as climate regimes or habitats. For example, a species that is widely distributed at low elevations in a mountain range when the climate is cool may move upward and form separate populations on different mountains when the climate becomes warmer. Exactly this pattern has been found for allopatric sister species of salamanders, which are found in locations with similar climate conditions and are absent from intervening regions with different climate conditions [47]. The number of species of birds, plants, and some other taxa is very high in mountainous regions such as the Andes, where many species have small ranges and are isolated by valleys from their sister species [25].

In allopatric speciation, isolating mechanisms evolve in geographically separated populations. They play a role in restricting gene flow only if the populations come back together, an event called **secondary contact**. This often happens as the range of one or both incipient species expands. The newly formed species can then coexist as distinct populations if they are sufficiently reproductively isolated.

If reproductive isolation is incomplete when secondary contact happens, three outcomes are possible. One is that the populations hybridize so freely that they meld back into a single population, and speciation fails. For example, this happened to incipient species of three-spined sticklebacks (*Gasterosteus aculeatus*) when the habitat changed and ecological selection against hybrids was alleviated

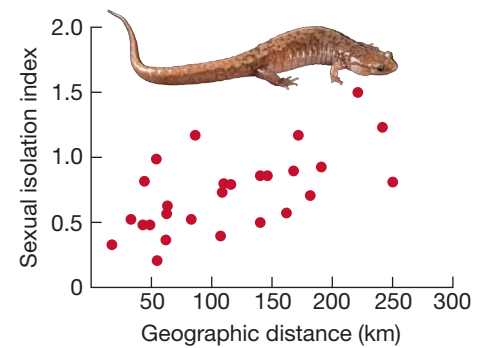


FIGURE 9.23 The strength of sexual isolation among populations of the salamander *Desmognathus ochrophaeus* is correlated with the geographic distance between the populations. The data are based on observations of mating behavior of pairs of salamanders in the laboratory. (After [102].)

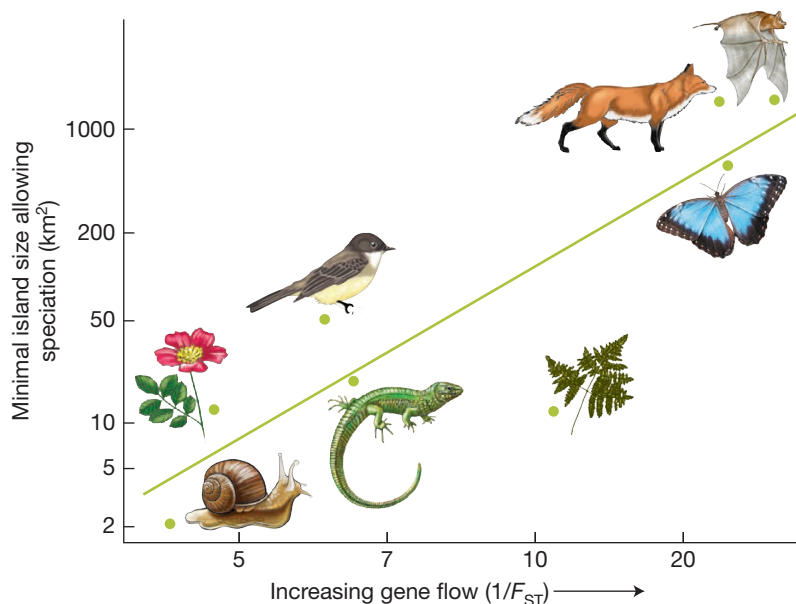


FIGURE 9.24 Speciation is more likely to occur on larger islands and in species with restricted gene flow. The minimal island size allowing speciation is small in taxa with low rates of gene flow, such as snails. Islands must be much larger for speciation to occur in taxa with high rates of gene flow, such as bats. Gene flow is measured here as $1/F_{ST}$ between populations ranging from 10 to 100 km apart. F_{ST} is a measure of genetic differentiation that decreases with greater gene flow (see Chapter 8). (After [43].)

[4]. A second outcome is that a hybrid zone is formed (for example, between the toads in Figure 9.4). Allele frequency clines are produced as alleles mix between the populations. Genetic differentiation may persist—perhaps indefinitely—for some parts of the genome because of selection, but other parts of the genome become homogenized by gene flow. We will return to this phenomenon below. A third outcome can happen when hybrids have low fitness, for example because of genetic incompatibility. Natural selection can then result in reinforcement of prezygotic isolation. Whether or not the newly formed species become sympatric can also depend on their ecological similarity. The two new species often use similar resources and live in similar habitats (see Chapter 13). Competition between them can be intense, and may prevent them from coexisting, or may even result in extinction of one of the species.

Sympatric speciation

The most extreme case of speciation with gene flow is sympatric speciation, which occurs when an ancestral population splits into two species without any geographic isolation (see Figure 9.22). In most scenarios, there is random mating at first. But in some cases gene flow might be reduced by an extrinsic factor (i.e., before any genetic divergence) even without geographic separation. For example, plants growing in different soils might be intermingled, but the soils might induce them to flower at different seasons, creating a temporal barrier to gene flow.

Sympatric speciation is controversial because interbreeding between the populations causes genetic mixing that can prevent the populations from diverging [24, 42]. Imagine a bird species that has disruptive selection on its bill. Birds with long thin bills eat insects, and birds with stout bills eat seeds (**FIGURE 9.25**). Birds with intermediate bills, however, have difficulty finding food and survive poorly. The

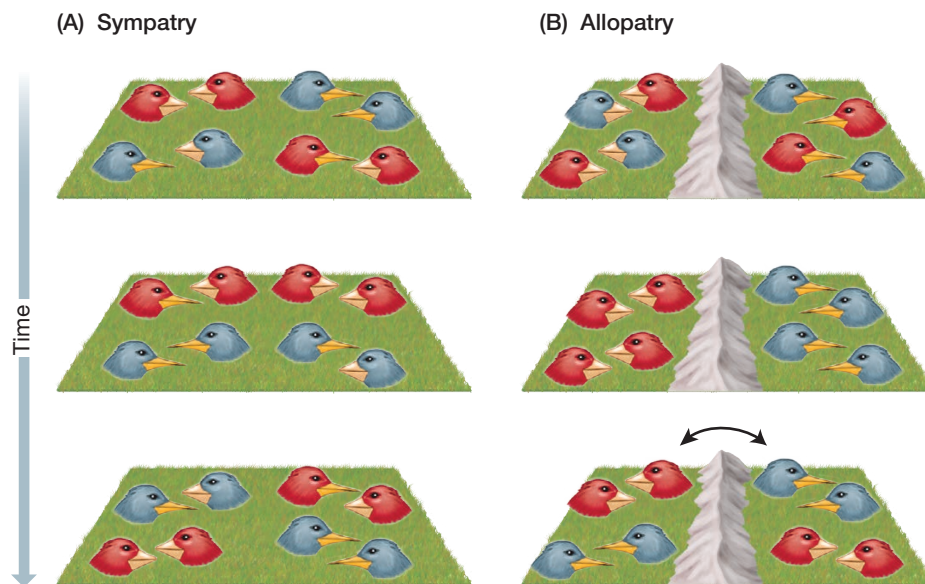


FIGURE 9.25 Sympatric speciation is less likely than allopatric speciation because recombination breaks down genetic combinations that might form new species. In this example, there are two morphs of a species of bird. Individuals with thin bills specialize on insects, while birds with stout bills specialize on seeds, and both forms have high fitness. Birds with intermediate bills, however, do not survive well. The birds choose mates on the basis of color: red mates with red, and blue mates with blue. (A) In sympatry, recombination erodes linkage disequilibrium

between the loci that affect color and bill size. This prevents the emergence of two species, for example a red bird with a stout bill and a blue bird with a thin bill, that would be separated by both prezygotic and postzygotic isolation. (B) With allopatry, geographically isolated populations can diverge both in traits that affect prezygotic isolation (such as color) and in traits that affect postzygotic isolation (such as bill size). If the differences are sufficient, the two populations will stay genetically distinct when they come into secondary contact. New species have formed.

birds also vary in color, and they mate *assortatively*: red birds tend to mate with red birds, and blue birds with blue birds. (Assortative mating could arise, for example, if young birds imprint on the color of their parents.) This situation provides the ingredients for speciation. If all the birds with thin bills are blue and all the birds with stout bills are red, the two populations have both prezygotic isolation (caused by assortative mating based on color) and postzygotic isolation (caused by selection against hybrids with intermediate bills). In this case, the alleles for color and bill size are in *linkage disequilibrium* (see Chapter 4), which causes the prezygotic and postzygotic reproductive barriers to reinforce each other.

Why would linkage disequilibrium develop between the color locus and the bill shape locus? Pairs of birds with the same type of bill (either thin or stout) will tend to have offspring with the same bill shape rather than an intermediate, disadvantageous bill. Pairs with the same type of bill are more likely to form if bill shape is correlated with color, the basis for assortative mating. Pairs that have the same color but different bill shapes will often produce progeny with intermediate bills and lower survival. Therefore, selection favors associations between color and bill-shape alleles (for example, red and stout alleles together, and blue and slender alleles together). In this way, selection can favor linkage disequilibrium between loci that contribute to prezygotic barriers and those that contribute to postzygotic barriers.

The difficulty for sympatric speciation is that if there is any continued interbreeding between birds with different combinations of alleles for color and bill shape, the linkage disequilibrium tends to be broken down. If linkage disequilibrium is not very strong to begin with, recombination erodes the buildup of advantageous combinations of alleles that can diverge into distinct populations and ultimately different species. This becomes an even greater problem if mating is based on several loci, because stronger selection is needed for all the color and bill shape loci to stay in linkage disequilibrium [24, 29]. Sympatric speciation can happen under the right conditions (strong disruptive selection and assortative mating), but those conditions are relatively rare. This is the basic reason that sympatric speciation is thought to be much less common than allopatric speciation.

Sympatric speciation is made much easier by a **speciation trait** (sometimes called a “magic trait”), namely a trait that causes *both* ecological divergence and reproductive isolation between the incipient species. This situation may occur frequently in insects that feed on a narrow range of host plants [5, 7]. Many herbivorous insects mate on the plants where they feed, ensuring that matings tend to be between individuals with the same host preference. Natural selection can favor mutations that strengthen the preference for a particular host (perhaps because that host is common), and as these mutations spread they will also strengthen prezygotic isolation from individuals that prefer other kinds of host plants. Reproductive and ecological isolation can build up this way to the point that what was a single species becomes two non-interbreeding populations, that is, new species. Populations that are at early and intermediate stages in this process are called “host races.” For example, the ancestor of the fly *Rhagoletis pomonella* laid eggs only in the fruit of hawthorns (FIGURE 9.26). In the late nineteenth century, the fly started to infest apple trees in the same areas as the normal host—and it is now known as the apple maggot. The flies mate on the host plant, and now consist of genetically divergent populations that differ in host preference and especially in their mating

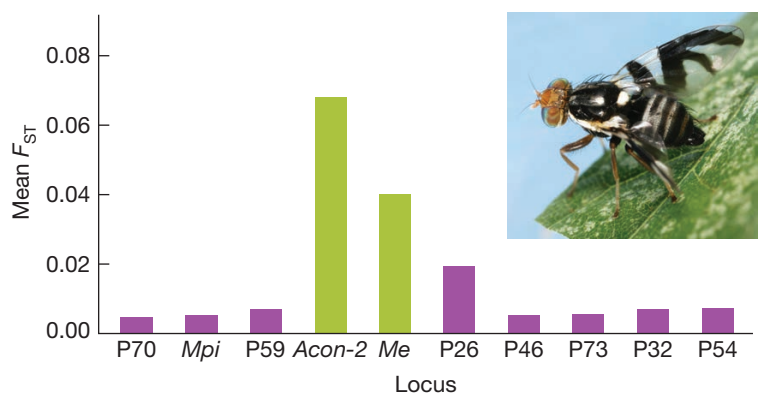


FIGURE 9.26 Genomic differences in the apple maggot fly (*Rhagoletis pomonella*), in which populations associated with different host plants have diverged by natural selection. The difference in allele frequency between the populations is measured as F_{ST} for several loci on one chromosome. Similar patterns were found for loci on the other chromosomes. Loci with significant allele frequency differences between samples from different host populations are shown in green. These loci and several of those shown in purple, are thought to be near genes that contribute to reproductive isolation. (After [61].)

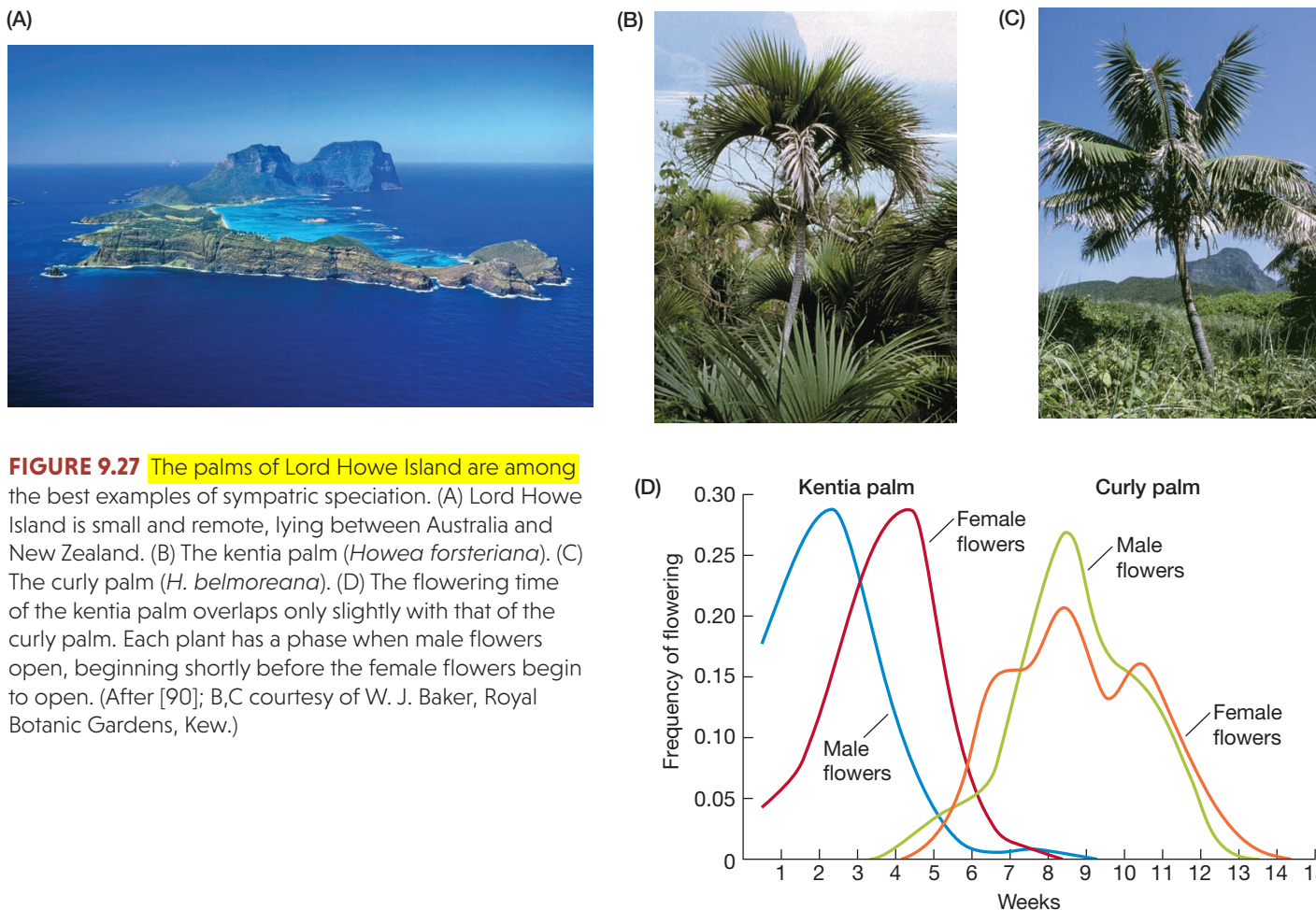


FIGURE 9.27 The palms of Lord Howe Island are among the best examples of sympatric speciation. (A) Lord Howe Island is small and remote, lying between Australia and New Zealand. (B) The kentia palm (*Howea forsteriana*). (C) The curly palm (*H. belmoreana*). (D) The flowering time of the kentia palm overlaps only slightly with that of the curly palm. Each plant has a phase when male flowers open, beginning shortly before the female flowers begin to open. (After [90]; B,C courtesy of W. J. Baker, Royal Botanic Gardens, Kew.)

season: their life cycle is timed to match the difference between fruit development of the two plants. Some of the difference in timing probably evolved in distant populations, with those alleles spreading to populations in apple-growing regions, where they enhance adaptation to apple [23].

The best evidence of sympatric speciation is provided by cases in which sister species occupy a small, isolated island or body of water that provides little opportunity for spatial separation of speciating populations. This is the case with several pairs of sister species of plants on Lord Howe Island, a small (15 km²) island in the South Pacific (FIGURE 9.27) [70]. More than one-third of the plant species on this island occur nowhere else in the world. Among these endemic species are the curly palm (*Howea belmoreana*) and its sister species, the kentia palm (*H. forsteriana*) [90]. The two species are often found growing in close proximity, and they are wind-pollinated, which makes it unlikely that there was ever a time when they were unable to exchange genes because of a physical barrier. The key difference between these palms is a 6-week difference in peak flowering time: cross-pollination can occur only for a short time, between relatively few plants (see Figure 9.27D). The kentia palm is found more often on calcareous soil than the curly palm. There may have been divergent selection for adaptation to calcareous versus noncalcareous soils. Moreover, the flowering time of the kentia palm is altered if it grows on noncalcareous soil.

How common is sympatric speciation? The answer varies substantially among groups of organisms [7, 15]. There are a fair number of possible cases of sympatric speciation in herbivorous insects, but only one example in birds: a seabird, the band-rumped storm-petrel (*Oceanodroma castro*; see Figure 9.9), which has split into sympatric populations with separate breeding seasons [28].

By contrast, perhaps as many as one-third of the endemic species of plants on Lord Howe Island may have originated there by sympatric speciation [70]. Most evolutionary biologists believe that allopatric speciation is much more common than sympatric speciation. Perhaps, though, many cases of sympatric speciation have gone undetected, because it is usually difficult to rule out a past history of allopatric divergence.

Parapatric speciation

An intermediate between allopatric speciation and sympatric speciation is parapatric speciation, in which neighboring populations diverge while they continue to interbreed (see Figure 9.22). We expect parapatric speciation to be more common than sympatric speciation because it involves less gene flow between the diverging populations.

Many examples have been described in which strongly selected genes and phenotypes differ between populations that interbreed [64]. Among these, a few indicate the evolution of some reproductive isolation that reduces gene exchange. For example, the White Sands region of New Mexico consists of dunes, formed less than 5000 years ago, that differ starkly from the surrounding dark soils. In three species of lizards that are distributed across both soil types, the populations that inhabit the dunes differ in head shape, toe length, and most strikingly in color—all characteristics that are adaptive and are thought to be strongly selected (**FIGURE 9.28**) [86]. In two of the species, a fence lizard (*Sceloporus undulatus*) and an earless lizard (*Holbrookia maculata*), there are strong differences in the frequencies of genetic markers across the boundary between the habitats. These genetic differences imply that gene flow has been reduced by the evolution of partial reproductive isolation. A likely reason is that the pale coloration is associated with differences in the color of ventral blotches that are displayed in sexual and other social encounters. Studies

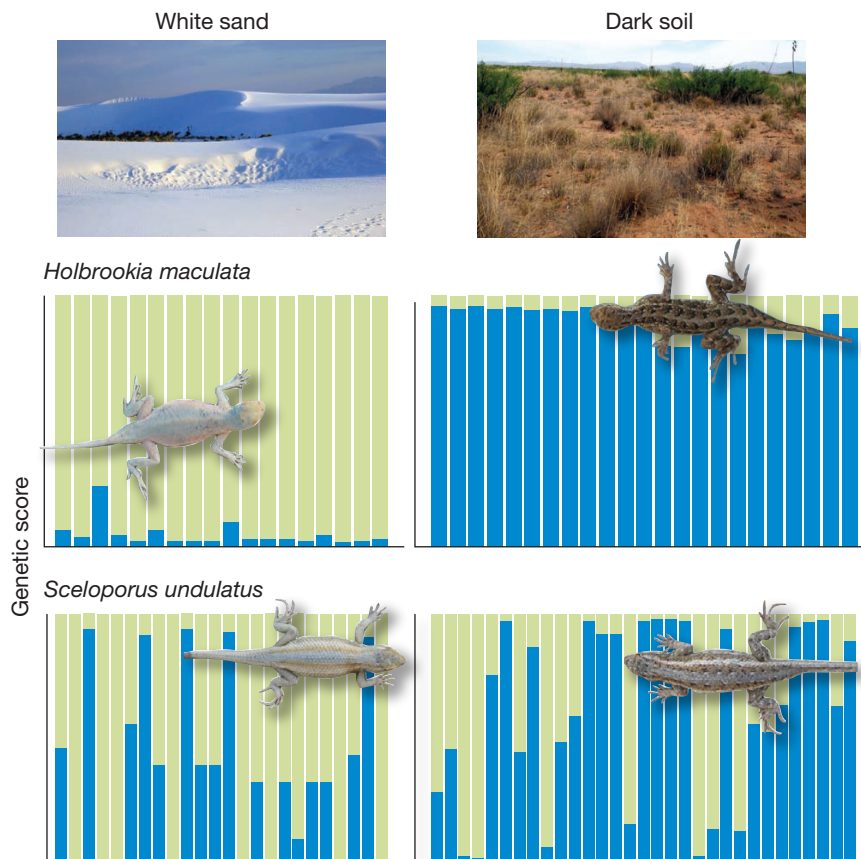


FIGURE 9.28 Incipient speciation with gene flow: divergence of lizards on the white sand and dark soil habitats shown in the photos at top. Multiple nuclear genes show that genotypes differ between habitats strongly in *Holbrookia maculata* and less so in *Sceloporus undulatus*. Each bar represents the genotype of one individual. The proportion of a bar that is green shows the probability, based on a lizard's genotype, that the individual belongs to a distinct white sand population, and the proportion that is blue that it belongs to a distinct dark soil population. Bars with intermediate amounts of green and blue indicate that the individual has a mixed genotype. (After [86].)

of mating behavior showed that partial sexual isolation has evolved in at least one of these species [34]. The level of genetic differentiation between the populations on white sands compared with those on normal soils is lowest in the whiptail lizard (*Aspidoscelis inornata*), the species that is most active and shows the highest level of gene flow among populations.

The Genomics of Speciation

As in all other fields in biology, the genomics revolution has opened up new perspectives on speciation. Genomics can help us determine the number, identities, and genomic locations of **speciation genes**, the loci that contributed to the evolution of reproductive isolation [64, 65].

When two populations or species are partly isolated but continue to hybridize, alleles introgress between them. The introgression, however, is expected to be uneven across the genome. In parts of the genome that are evolving neutrally, gene flow between the populations will tend to make them more similar. In addition, if a mutation appears in one species that is beneficial to both species, it will sweep through both and homogenize that region of the genome between the species. Earlier in this chapter, we saw that genes for warning colors in *Heliconius* butterflies have spread among species this way (see Figure 9.5) [35].

A contrasting picture is expected in genomic regions that carry loci that isolate hybridizing species. Those regions, sometimes called “genomic islands of speciation,” are expected to show greater genetic divergence than the rest of the genome. The group of mosquitoes that transmit malaria in Africa (genus *Anopheles*) includes six species that diverged recently and that continue to hybridize [26]. Comparisons of the genomes reveal some regions (particularly inversions) that are similar in some species pairs because they have introgressed following hybridization, like the color pattern genes in *Heliconius* butterflies. But other regions of the *Anopheles* genome show unusually high divergence among species—the signature of speciation genes. In particular, the X chromosome is more genetically different than the autosomes. It has deep gene trees (see Chapter 7), which strongly suggests that genes on the X chromosome were among the first to contribute to reproductive isolation during the speciation process (see Figure 16.11). That pattern is consistent with the observation that sex chromosomes often play a disproportionately large role in the evolution of reproductive isolation [15].

Genomic islands of speciation might provide evidence about the geography of speciation, but this is still uncertain. Genomic islands are predicted to develop during speciation with gene flow. They will also appear when two populations that speciated in allopatry come back into contact and then hybridize [19]. Allopatric populations will show different genomic “islands” at sites where divergent natural selection fixed different alleles that may or may not make a potential contribution to reproductive isolation. If these populations expand and hybridize, divergent selection will maintain the adaptive differences between the hybridizing populations, while neutral regions introgress and become homogenized between the populations. Distinguishing speciation with gene flow from secondary contact presents the same difficulty as determining whether sympatric species originated sympatrically or became sympatric by secondary contact after speciation happened allopatrically. Deciding between those possibilities requires additional evidence.

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SUMMARY

- Several definitions of "species" have been proposed. Most evolutionary biologists use the biological species concept, which defines species as groups of actually or potentially interbreeding organisms that are reproductively isolated from other such groups, meaning they do not (or would not) exchange genes even if they encounter each other. Under this definition, speciation is the evolution of reproductive isolation. Some other biologists favor the phylogenetic species concept, according to which species are sets of populations with character states that distinguish them.
- Under any definition of species, the defining qualities (such as reproductive isolation) usually evolve gradually, so some populations cannot be clearly classified as the same or different species.
- The biological differences that constitute reproductive isolation include prezygotic barriers to gene exchange (e.g., ecological or sexual isolation) and postzygotic barriers (hybrid inviability or sterility). Several potential isolating barriers may be discovered between two species. Some of them may have evolved before the others, and been the actual basis of speciation. Some barriers (e.g., postzygotic barriers) may not come into play because an earlier-acting difference already prevents gene exchange.
- Speciation is rapid in some cases, requiring only a few thousand years or even less. Partial reproductive isolation has evolved even in laboratory populations. Occasionally, a new species is generated instantly by whole genome duplication. In other cases, it may take millions of years for populations to evolve reproductive isolation.
- The causes of the evolution of prezygotic reproductive isolation include divergent natural selection arising from ecological factors (ecological speciation) and divergent sexual selection. When hybrids between two divergent populations have low fitness, there is selection for stronger prezygotic isolation, which may result in reinforcement of a prezygotic barrier.
- The causes of evolution of postzygotic isolation are less well understood. Hybrid inviability and sterility are often based on incompatible interactions among two or more genetic loci that diverged between populations by genetic conflict or divergent selection. Hybrid sterility can also be caused by differences in the numbers or arrangements of chromosomes. In some cases, these chromosome differences may have been established by random genetic drift.
- New species sometimes evolve from hybrids between parent species. In many cases, the hybrid species is polyploid.
- Evolutionary biologists agree that allopatric speciation is common. Here a physical barrier separates populations of an ancestral species, and evolutionary changes in one or both populations result in biological barriers to gene flow if the populations come back into contact. One possible mode of allopatric speciation, peripatric or founder effect speciation, is thought to be initiated by genetic drift in a small local population of an ancestral species. This is generally thought to be rare.
- In speciation with gene flow, a species evolves into two species because of strong divergent selection, without a physical barrier between populations. The evolution of reproductive isolation is hindered by ongoing interbreeding (which maintains gene exchange) and recombination (which opposes the buildup of divergent sets of genes and characteristics).
- Sympatric speciation is the evolution of reproductive isolation within an initially randomly mating population. It is the most extreme instance of speciation with gene flow, and requires very strong selection. It is made more likely if traits that are disruptively selected because of their ecological function also automatically reduce gene exchange (e.g., seasonal timing of reproduction).

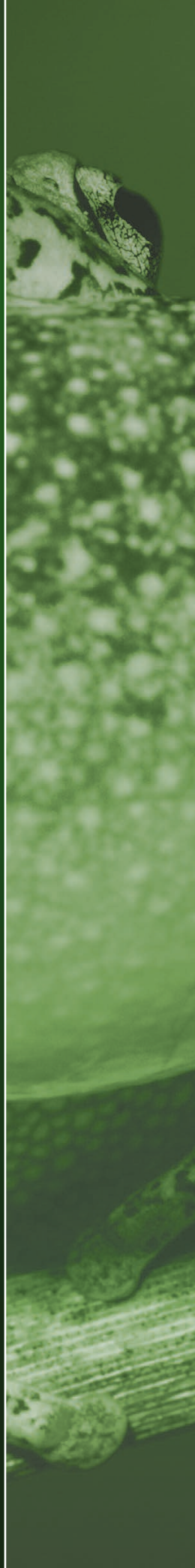
TERMS AND CONCEPTS

allopatric
allopatric speciation
biological species
concept (BSC)
dispersal
Dobzhansky-Muller
incompatibility
(DMI)

ecological isolation
ecological
speciation
epistasis
founder effect
genetic conflict
Haldane's rule

hybrid zone
introgression
(introgressive
hybridization)
inversion
isolating mechanism
parapatric

parapatric
speciation
peripatric speciation
phylogenetic
species concept
(PSC)
postzygotic barrier
prezygotic barrier





reciprocal
translocation
reinforcement
reproductive
isolating barrier
(RIB)

reproductive
isolation
secondary contact
segregation
distortion
sexual isolation

sister species
speciation
speciation gene (and
speciation trait)
speciation with gene
flow

sympatric
sympatric speciation
vicariance

SUGGESTIONS FOR FURTHER READING

Speciation, by J. A. Coyne and H. A. Orr (Sinauer Associates, Sunderland, MA, 2004) is the most recent comprehensive book about speciation.

Ecological Speciation, by P. Nosil (Oxford University Press, New York, 2010) is a short but comprehensive treatment of speciation caused by divergent environmental selection.

The Ecology of Adaptive Radiation, by D. Schluter (Oxford University Press, New York, 2000) discusses ecological aspects of speciation and its relationship to adaptive radiation.

Useful overviews and reviews include:

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PROBLEMS AND DISCUSSION TOPICS

1. Some degree of genetic exchange occurs in bacteria, which reproduce mostly asexually. What evolutionary factors should be considered in debating whether or not the biological species concept (BSC) can be applied to bacteria?
2. Suppose the phylogenetic species concept (PSC) were preferred over other species concepts, such as the BSC. What would be the implications for (a) discourse on the evolutionary mechanisms of speciation; (b) studies of species diversity in ecological communities; (c) estimates of species diversity on a worldwide basis; and (d) conservation practices under such legal frameworks as the U.S. Endangered Species Act?
3. How might the fate of two hybridizing populations—that is, whether or not they persist as distinct populations—depend on the kinds of isolating barriers that reduce gene exchange between them?
4. The heritability of an animal's preference for different habitats or host plants might be high or low. How might heritability affect the likelihood of sympatric speciation by divergence in habitat or host preference?
5. Three-spined sticklebacks that have colonized freshwater streams and lakes have repeatedly evolved into similar forms. The pattern can be seen in hundreds of freshwater bodies around the world. Can a single biological species arise more than once (i.e., polyphyletically)? How might this possibility depend on the nature of the reproductive barrier between such a species and its closest relative?
6. If a researcher discovers regions of genome in a set of hybridizing populations that have much higher F_{ST} than the rest of the genome, what alternative hypotheses must be considered before concluding that these regions are "genomic islands of speciation"? How might a researcher distinguish these hypotheses?